

**THE EFFECTS OF COMPETITION AND LARVAL HABITATS ON POPULATIONS
OF THE AUSTRALIAN SHEEP BLOWFLY *LUCILIA CUPRINA* (WIEDEMANN).**

by
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Submitted in fulfilment of the requirements for the degree
of Doctorate of Philosophy.

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Except as stated herein this thesis contains no material which has been accepted for the award of any other degree or diploma in any university, and that, to the best of my knowledge and belief, the thesis contains no copy or paraphrase of material previously published or written by another person, except when due reference is made in the text.

A handwritten signature in cursive script, reading "Howel Williams". The ink is dark and the handwriting is fluid, with the first letters of each word being capitalized and prominent.

Howel Williams.

Typographical corrections.

Cont. p6 ln 2 - sp. delays
Sum p2 ln 10 - sp. tends to suppress
page 2 ln 7 - sp. Meigen
page 3 ln 7 - rep. Mormoniella with Nasonia
page 6 ln 6 - delete 'Fungal '
page 6 ln 17 - sp. predisposing
page 6 ln 21 - sp. operation
page 7 ln 15 - sp. blowflies
page 9 ln 4 - rep. Mormoniella with Nasonia
page 9 ln 19 - ins. '.'
page 23 ln 8 - sp. sulphide
page 24 ln 15 - sp. 3.1.2.1
page 41 ln 6 - sp. was
page 46 ln 1 - ins. '3.2'
page 80 ln 19 - sp. differential
page 100 ln 1 - sp. Polwarth
page 100 ln 11 - sp. trays
page 105 ln 12 - sp. occurred
page 112 ln 17 - sp. proportional
page 113 ln 10 - delete 'reationship'
page 120 ln 3 - sp. occurred
page 123 ln 11 - delete 'from'
page 126 ln 3 - ins. '.'
page 127 ln 3 - delete 'a'
page 141 ln 20 - reverse authors
page 141 ln 22 - sp. sources
page 147 ln 14 - sp. distances
page 153 ln 3 - sp. occurred
page 157 ln (last) - ins 'is'
page 166 ln 1 - sp. larval
page 175 ln 9 - sp. successful
page 178 ln 5 - sp. occurring
page 178 ln 13 - sp. were
page 182 ln 11 - sp. unsuccessful
page 193 ln(last) - sp. Temporal

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SUMMARY

The effects of competition on *Lucilia cuprina* with particular reference to the success of this species in carrion breeding in Tasmania was investigated. The spatial and temporal interaction of the necrophagous fly guild was studied in the main sheep raising areas of the state, and laboratory studies were used to examine the effects of larval competition on life history parameters.

The field study showed that *Chrysomya rufifacies* and *Chrysomya varipes* had a restricted distribution both geographically (occurring in the northern and central areas of the state) and seasonally (first occurrence being usually in mid- to late summer). This was thought to have particular significance to the success of *L. cuprina* breeding in carrion as the presence of these species tends to suppress the number of its larvae emerging from carrion. A series of carrion experiments were designed to assess the success rate of *L. cuprina* breeding in the presence and absence of *Ch. rufifacies*. It was found that in the absence of *Ch. rufifacies* some *L. cuprina* were seen to emerge from carrion. The temperatures generated within a carcass were monitored and although high temperatures were generated they were within the thermal tolerance of *L. cuprina*. There was no correlation between the abundance of species emerging and the abundance of species trapped adjacent to the carcasses.

The fine scale distribution of *L. cuprina* was found to be highly correlated with the presence of both live sheep and sheep carcasses. It had a strongly clumped distribution with several strong nodes of abundance within the trapping area (1km² of sheep pasture). All of the other species studied showed a high correlation with sheep carcasses but not with live sheep.

Laboratory studies were conducted to simulate competition in both carrion and myiasis. These studies showed that *L. cuprina* had a considerable capacity for compensating preadult mortality by sacrificing adult size. In artificial carrion, adult size and mortality (preadult and adult) were found to be related to the initial larval density. Development rates were generally increased with decreased adult size.

Induced myiasis using a range of larval densities showed that adult size and preadult mortality were independent of initial density. Flies emerging from the induced myiasis experiments were in the larger range of adult sizes. Flies emerging from the artificial carrion experiments covered the whole range of adult sizes. This observation led to the analysis of the field population for size related effects of competition.

It was suggested that the general size distribution of flies was related to the alternative larval habitats. Using this general rule it was concluded that at least 18% of the field population studied originated from conditions of high larval densities and therefore, probably from carrion breeding. This conclusion was supported by the observation that the size distribution of adult *L. cuprina* emerging from carrion reflected high larval densities. A high proportion of the population was found to be resorbing eggs and this was assumed to indicate a severe shortage of suitable oviposition sites.

A major study of the size and age composition of the field populations of *L. cuprina* was done in the hope that useful data relating to the characterisation of cohorts could be found. This work was largely unsuccessful due mainly to inherent errors in the aging technique.

A simple simulation model was constructed to assess the affects of larval competition on the reproductive fitness of the adult population. This showed that potential reproductive fitness increased with increased competition (and consequently decreased adult size). This result demonstrated that competition occurring in carrion may increase the reproductive potential of the flies emerging, although other factors such as mobility (and thus the probability of a successful oviposition) may be reduced. It was concluded that factors other than adult size (such as number and reproductive potential) should be considered when assessing the contribution of carrion breeding to the persistence of *L. cuprina* populations.

CHAPTER 1

GENERAL INTRODUCTION

1.0 INTRODUCTION

The Calliphoridae are a large cosmopolitan group of flies. Of the Australian assemblage approximately 4% have been introduced since European settlement 200 years ago (CSIRO, 1979). In contrast to most other groups of flies, it is the larval form rather than the adult which is of economic importance as a vector of disease or a cause of damage to livestock. The species constituting the necrophagous fly guild in Australia are from two sub-families of the Calliphoridae: the Calliphorinae (of which 20-30% of the necrophagous forms are introduced) and the endemic Chrysomyinae.

The Calliphorinae are the most important component of the decay community in carrion (Bornemissza, 1957; Payne, 1965; Putman, 1978); most other insect groups (including the Chrysomyinae) are present in carrion as predators of the Calliphorinae (Putman, 1978). The larval forms however are also often involved in cutaneous myiasis (or "strike") (CSIRO, 1979) a habit which is thought to be a natural extension from carrion breeding (Zumpt, 1965).

1.1 MYIASIS

1.1.1 HISTORY

The first records of strike in Australia come from Tasmania and date from before the 1870's (Joint Blowfly Committee, 1933). The flies involved in these incidents were probably *Calliphora stygia* (Fabricius) and did not present a great problem to the local wool industry at that time. On the Australian mainland, strike was first recorded in 1883 from Queensland, but the problem did not become widespread or frequent until 1903 in the

Riverina district (Joint Blowfly Committee, 1933). With the increasing incidence of strike attention was given to identifying the species involved.

Froggatt (1904) implicated *Calliphora oceanicae* (Desvoidy) [later identified as *Calliphora augur* (Fabricius) by Mackerras and Fuller (1937)]. From that time to the early 1930's many species were identified as the principal cause of myiasis [for examples see Froggatt (1915)], but by the end of this period the general consensus of opinion blamed *Lucilia sericata* (Meigen) (Anon, 1930), the principal species involved in strike in Great Britain (Salt, 1932; Cragg, 1955).

The Joint Blowfly Committee (1933) implicated both *Lucilia cuprina* (Wiedemann) and *L. sericata* as principals in strike. Finally *L. cuprina* was identified as the sole principal in strike by Mackerras (1936). This conclusion was supported later by surveys of the species composition of strikes by Mackerras and Fuller (1937). Recent surveys of the same nature have reaffirmed the dominant role played by *L. cuprina* in cutaneous myiasis (Watts *et.al.*, 1976; Barton, 1981).

There was confusion about the taxonomic status and identification of *L. cuprina* and *L. sericata* until Waterhouse and Paramonov (1950) established them as separate species. However, *L. sericata* and *L. cuprina* are still treated as variants of one species by some South African workers (Kitching, 1981). *L. cuprina* was probably introduced into the Australian mainland in the late 1800's from South Africa or India (Waterhouse and Paramonov, 1950). Its introduction into Tasmania was comparatively recent, the first record being by Ryan (1954) in 1949-50. In contrast, *L. sericata* was recorded as being present in Tasmania prior to this time (Waterhouse and Paramonov, 1950).

The current estimate of the cost to the Australian wool industry through damage

caused by *L. cuprina* is of the order of \$100 million per annum (Barton 1981); research into control of the problem has been going on since the 1920's.

1.1.2 CONTROL

Research into the control of *L. cuprina* can be divided into the following three broad categories.

1.1.2.1 Reduction or eradication of pest species populations

Early interest in biological control focused on the introduction of parasitoids and other natural enemies and was reviewed by Anon. (1930) and the Joint Blowfly Committee (1933). Particular interest was devoted to the use of a native Chalcid wasp *Nasonia vitripennis* Walker and the introduction of the Braconid wasp *Alysia manducator* Pantzer. No biological agents with a significant effect on *L. cuprina* populations have been found to date (Norris, 1959) and this line of research has dwindled since the late 1930's. However, recent interest has been concentrated on the development of pathogenic, parasitic nematodes of *L. cuprina* (Bedding, 1983).

Trapping, as a means of reducing local populations was proposed by Mackerras *et.al.* (1936). The underlying supposition in this approach was that strike incidence and fly numbers were positively correlated, a view supported by Mackerras (1936). However, trapping was expensive at the time that this research was performed and is even more so now. Furthermore, it has been shown that strike incidence is correlated to the susceptibility of the sheep rather than fly numbers (Wardhaugh pers. comm.).

The destruction of carcasses to reduce breeding sites for *L. cuprina* was advocated as an early control measure by Gurney and Woodhill (1926). The impracticality of this approach was demonstrated by Fuller (1932a), who found that burial favoured the

development of primary flies. Further problems have been identified, the major one being that it is unlikely that carcasses will be found and destroyed before a significant number of primary flies have completed their development (Joint Blowfly Committee, 1933).

Another control measure of recent interest has been the induction of immunity in the host by the production of larval antigens; this however has had no effect on larval survival on sheep (O'Donnell *et.al.*, 1981).

Current research has concentrated on the genetic manipulation of fly populations. The approaches under development are: the use of semi-sterile compound chromosome strains to replace local populations; female killing systems; conditional lethal strains; and sterile male releases (Whitten *et.al.*, 1977). However, all these systems have been costly to develop and no effective controls have been demonstrated with *L. cuprina* to date.

1.1.2.2 Intervention in the development of strikes

This approach is mainly represented by the use of insecticides to stop or inhibit oviposition and larval development of *L. cuprina* on sheep. There was a spectacular initial success with the use of Dieldrin (Norris, 1959), followed by the rapid development of resistance in populations. Treatments have also been developed to control strikes that are already established. To act effectively on blowfly populations this approach requires early treatment of developing strikes, and jetting of flocks before, or soon after, a sheep blowfly wave has been noticed.

Early treatment relies on early identification of struck animals; it is therefore, useless for covert strikes (small and sometimes chronic strikes not usually identified by yarding and inspection of sheep) due to their very nature of being hard to detect under normal stock inspection conditions. It is unlikely therefore that these measures (such as

field dressings) will have any impact on blowfly populations and they will remain as a last course of treatment for animals already struck. However, the development of oviposition suppressants promises great potential in control (Orton and Shipp, 1983).

1.1.2.3 Prophylactic treatment

Underlying this approach has been the identification of the predisposing factors contributing to the susceptibility of the host.

Froggatt (1915) noted that the Merino was susceptible because of artificial selection for high yields of fine wool, its wrinkled skin, and high yolk content. In an extension to this, Hayman (1953) suggested that wool density was the most important factor in susceptibility. Holdaway and Mulhearn (1934) loosely correlated "weather stain" and yolk content with susceptibility to strike.

Mackerras (1936) made the observation that warm and humid weather appeared to be correlated to the incidence of strike. Hall, Martin and McDonell (1980) reported an incidence of 1% strike in dry woolled strains and 30% in moist wool. They also related frequency of strike to sites on the body, and found that the moistest areas such as the shoulders were struck most often. All these factors contribute to conditions which predispose the fleece to bacterial and fungal infections, and the creation of microhabitats suitable for the development of larvae.

Merritt and Watts (1978a) demonstrated that wetting a fleece promoted the growth of a bacteria, *Pseudomonas* spp. (the causal agent of "fleece-rot"). Later, Watts, Merritt and Goodrich (1981) found that wool infected with *Pseudomonas aeruginosa* provided a strong stimulus for oviposition in *L. cuprina* and that in comparison, wet wool alone provided no stimulus.

Whilst pure cultures in wool of the bacteria *Bacillus subtilis* (Merritt and Watts, 1978b), *Enterobacter cloacae*, and *Proteus mirabilis* (Emmens and Murray, 1982) have been shown to stimulate oviposition in *L. cuprina*, it has been suggested that the synergistic effects of *P. aeruginosa* with these other bacteria provides the principal stimulus to *L. cuprina* (Emmens and Murray, 1983).

Infections in the form of dermatophilosis ("lumpy wool") induced by *Dermatophilus congolensis* and in the presence of *Pseudomonas* spp. have also been shown to promote oviposition in *L. cuprina* (Gherardi *et.al.*, 1981). In field studies, Gherardi *et.al.* (1982) found that larger proportions of strike occurred in groups of sheep infected with *D. congolensis* alone, or mixes of *D. congolensis* with *Pseudomonas* spp., than groups infected with *Pseudomonas* spp. alone.

Murray (1980), in a survey of flocks in Victoria, found that breech strike in response to scouring was the most common type of myiasis, followed by body strike usually related to "fleece-rot". Other factors such as helminth infestation resulting in breech soiling, have been related to susceptibility to breech strike (Morley *et.al.*, 1976; Murray, 1980).

Against this collection of predisposing factors there are some effective control measures. To prevent scouring, treatment of helminth infestations, and care with the sheep's diet are necessary. However, to reduce breech strike significantly, tail docking and mulesing have been recommended for a long time (Graham, Johnston and Riches, 1947). The recent adoption of the radical mules operation has been reported to reduce breech strike by up to 80%, by Watts, Murray and Graham (1979). The apparent cruelty of the operation and the unfounded idea that it results in reduced growth rates, has led to a

low rate of mulesing in Tasmania (Reid and Jones, 1976).

Work on the control of bacterial and fungal predisposing conditions is under way and will be of significance in the future (Burrell, 1983).

The problem of myiasis is mainly related to two conflicting factors. These are:

- i), that artificial selection of sheep is aimed at maximising production,
- and ii), sheep that are favoured in this way are usually the most susceptible to strike.

Because of this relationship, it has been prophylactic approaches aimed at susceptible sheep that have been the most successful in reducing the incidence of strike. But it should be noted that research has now focused on breeding less susceptible sheep. The approach adopted is to select for increasing resistance to fleece-rot (McGuirk, 1983), rather than correcting the conditions resulting in susceptibility, that is, the underlying conformation of the sheep. It is probable that in the future any other viable means of controlling *L. cuprina* populations, such as genetic control, will be secondary to the prophylactic approach in an integrated management plan.

1.2 INTERACTION OF *LUCILIA CUPRINA* WITH OTHER BLOW FLIES

Lucilia cuprina is attracted both to live sheep and carrion as potential breeding sites. Bacterial odours emanating from lesions on susceptible sheep and carrion are similar and account for this attraction (Emmens and Murray, 1983). Of the flies attracted to live sheep, *L. cuprina* is the only one to lay eggs readily (Mackerras and Mackerras, 1944), and is most often found as the sole species in strikes (Mackerras and Fuller, 1937; Watts *et.al.*, 1976). The action of *L. cuprina* in laying eggs may stimulate egg laying by flies of the same species (Barton-Browne, van Gerwen and Williams, 1979), or by other species (Waterhouse and Paramonov, 1950). The later stages of development of strikes make

wounds attractive to secondary and tertiary species.

1.2.1 INTERACTION IN CARRION

Fuller (1932b) listed *L. cuprina*, *L. sericata*, *C. stygia*, *C. augur*, and *Calliphora fallax* [=hilli Patton] as constituting the primary flies visiting carrion; *Calliphora albifrontalis* [=australis Malloch], *Calliphora nociva* Hardy, and *C. vicina* have been added by Norris (1959).

Lucilia cuprina is attracted to carrion for protein for egg development [like most Calliphoridae it is anautogenic, that is, unable to develop eggs without a protein meal, (Webber, 1955; Kitching, 1981)], probably as a site for mating (Barton-Browne *et al.*, 1976), and as a potential larval food resource. More gravid *L. cuprina* visit carrion than live sheep (Woodburn and Vogt, 1982), due in part to the stronger degree and range of attraction of carrion compared with that of struck, or susceptible sheep (Mackerras and Mackerras, 1944).

Ullyett (1950) suggested that of the species making up the South African necrophagous fly guild, *Lucilia* spp. were the best adapted to inter- and intra-specific competition. He suggested that this was due to the mortality of the pupal stage being independent of crowding in the larval stage. In contrast, Fuller (1934) found that whilst *L. cuprina* and *L. sericata* bred primarily in carrion, *L. cuprina* was not very successful due to intense intra-specific competition and inter-specific competition from other *Calliphora* spp., a factor also recognised by Anon (1930) the Joint Blowfly Committee (1933) and Mackerras (1936). This severe competition results from the overblowing of carcasses (due to the great attraction of carrion and the number of species involved), and appears to be normal (Norris, 1965).

As well as competition there is heavy predation of primary fly larvae by the carnivorous larvae of *Chrysomya rufifacies* (Macquart) (Fuller, 1934; Waterhouse, 1947); beetles from the families Staphylinidae, Histeridae, and Silphidae (Kitching, 1981); and Hymenopteran scavengers and parasitoids (notably *N. vitripennis*) (Froggatt, 1915; Salt, 1932; Joint Blowfly Committee, 1933; Fuller, 1934; Bornemissza, 1957; Norris, 1959). Carrion is made still more unfavourable to *L. cuprina* by the generation (by other calliphorids and *Ch. rufifacies*) of temperatures in the carcass above its thermal tolerance (Waterhouse, 1947).

Interference by vertebrate scavengers such as birds and mammalian carnivores, may also be important in reducing the success of *L. cuprina* in carrion (Froggatt, 1915). The overall mortality of larvae leaving carcasses was estimated to be 98% by Waterhouse (1947). In Victoria, Barton (1981), proposed that carcasses only produced significant numbers of *L. cuprina* in the late summer-autumn season, due principally to the absence of *Ch. rufifacies* in carrion at this time.

1.2.2 INTERACTION IN MYIASIS

Lucilia cuprina is significantly more successful in myiasis than in carrion (Vogt and Woodburn, 1979). This is due to a relative lack of inter-specific competition for food, resulting from *L. cuprina*'s strong attraction to live sheep and readiness to lay eggs in comparison to other flies and the reduced incidence of *Chrysomya rufifacies*.

Waterhouse (1947) showed that temperatures occurring during myiasis are more favourable to *L. cuprina*; and suggested that the developing larvae can regulate their temperature by movement up and down the wool staples. The incidence of parasitism in wandering larvae is low because live sheep do not act as a fixed point of strong attraction to predators or parasitoids as does carrion. It has recently been recognized that covert

strike probably represents an important input into the local population (Wardhaugh and Dallwitz, 1983).

1.2.3 STATUS OF *LUCILIA CUPRINA* IN TASMANIA

In Tasmania it has been found that *Ch. rufifacies* is not present for the same period as it is on the mainland. It is probable that this species migrates across Bass Strait, resulting in transient populations on the Tasmanian mainland (McQuillan, Jones and Williams, 1983). Migration of *Ch. rufifacies* to Tasmania has been suggested by McQuillan, Jones and Williams (1983) because of the correlation of the occurrence of *Ch. rufifacies* with the spring migration of *Musca vetustissima* Walker.

Hughes (1970) related the migration of *M. vetustissima* to warm anticyclonic airflows occurring ahead of cold fronts; this meteorological condition is now known to account for a large influx of insects into Tasmania in spring (Drake *et.al.*, 1981). *Ch. rufifacies* arrives late in summer and at unpredictable times in Tasmania. The southern-most record of *Ch. rufifacies* is at Ross in central Tasmania, (Williams, in prep.), and it seems that this species is not present in Tasmania long enough for it to penetrate further south than this point.

It is therefore possible that *Ch. rufifacies* is not acting in its key role of governing the success of *L. cuprina* in carrion during late spring and early summer in northern Tasmania, or during the whole period of *L. cuprina*'s activity in southern Tasmania. Williams and Richardson (1983) have shown that in the absence of *Ch. rufifacies*, *L. cuprina* is the best adapted member of the necrophagous fly guild in Tasmania to exploit carrion, based on comparisons of the flies' ability to tolerate high temperatures and cope with strong inter- and intra-specific competition. Temperature tolerance and competitive ability are the two principal criteria (after the presence of *Ch. rufifacies*) used to explain the

absence of *L. cuprina* in carrion on the Australian mainland (Waterhouse, 1947; Mackerras, 1936; Ryan, 1954). There is also difficulty in determining what is a significant contribution from carrion to the *L. cuprina* population. As Norris (1959) suggested, a regional population of *L. cuprina* may persist through breeding in carrion in the absence of myiasis.

Another contrast between the Tasmanian scene and the Australian mainland is the different status of *L. sericata*. The distribution of *L. cuprina* and *L. sericata* on the Australian mainland is quite distinct, with *L. cuprina* occurring as a rural fly and *L. sericata* in urban and coastal areas (Joint Blowfly Committee, 1933). Waterhouse and Paramonov (1950) put this down to the humidity tolerances of the flies; *i.e.* *L. cuprina* can tolerate semi-arid conditions whilst *L. sericata* occurs typically in habitats with high relative humidities. They also correlated the distribution of *L. cuprina* with the presence of sheep. In contrast, *L. sericata* occurs in high densities in rural areas in Tasmania (McQuillan, Jones and Williams, 1983). Associated with this is a high incidence of *L. sericata* in strikes, although this species is not thought to initiate any (Watts *et al.*, 1976).

1.3 COMPETITION AND PHENOTYPIC PLASTICITY

Collins (1980), proposed that the "degree to which a life history feature deteriorates in response to realistically applied, naturally occurring stresses should be an inverse measure of the importance of that parameter to fitness". As a corollary to this he suggested that under the assumption that fitness is expressed in terms of population growth rate, then those features that deteriorate little should be those that have the greatest effect on the population growth in nature.

The response of flies to competition for a limited food source in the larval stage is to exhibit a plasticity in the range of sizes over which viable pupae, and thus adults, can be

formed. Plasticity in viable pupal size offsets mortality that would otherwise result if the larvae had to reach a target size in order to complete development (Nicholson, 1950).

Reduction in size results in reduction in fecundity; however, an otherwise high risk of mortality in the prereproductive stage is moderated (Collins, 1980). Mortality in the late larval period is the most significant contributor to overall mortality in a blowfly's life cycle [Putman (1977) estimated a pre-adult mortality rate of 80% in *C. vicina*].

An evolutionary mechanism which promotes the development of phenotypic plasticity in populations has been discussed by Kaplan and Cooper (1984). This mechanism is decanalizing selection, a selective process which favours the development of genotypes where phenotypic plasticity itself is an inherited character. Decanalizing selection acts most effectively on organisms with un-buffered developmental systems (that is, the outcome of development is dependent on environmental conditions) occurring in fluctuating environments. In the case of blowflies, plasticity in size enhances the survival of larvae through to the adult stage in an environment in which competition is variable.

Williams and Richardson (1983) suggested that the degree of plasticity in size is an indication of the extent to which inter- and/or intra- specific competition occurs in the larval habitat. They found a broad range of viable sizes in *L. cuprina*, *L. sericata*, and *C. vicina*; but a comparatively narrower range in other Tasmanian necrophagous flies. So, whilst variable levels of competition, and thus decanalizing selection, probably act on all blowfly species, it has acted strongly on *L. cuprina*, *L. sericata*, and *C. vicina*; resulting in their comparatively high plasticity in size.

As has been mentioned above there is a general species specific effect of reduced fecundity with decreased size; however, the situation is more complex when the

relationship of the ratio of reproductive tissue weight to total body weight is considered. This relationship has been found to behave differently in different species (Williams and Richardson, 1983; Williams and Richardson, 1984). Generally the *Calliphora* spp. show little change in the ratio with changes in adult size. However, *L. cuprina* shows a large increase in the relative proportion of reproductive tissue with decreased adult size.

Roff (1977) found that the energetic and reproductive costs of dispersal increased with decreasing size in *Drosophila melanogaster*. Furthermore there is a general effect of size on flight efficiency in insects (Unwin and Corbet, 1984). These relationships are modified further when the ratio of reproductive tissue to body weight is considered, and may have significant effects on populations.

Further effects of variable adult size have been found in *M. vetustissima* with longevity (Sands and Hughes, 1977; Hughes, 1977a), and egg development rates (Hughes, 1974) increasing with increased adult size.

1.4 THE PRESENT STUDY

It is apparent that there is an extensive literature concerning *L. cuprina* and sheep strike in Australia. Much of this research was done in the first half of this century and the broad generalisations arising from this work have by now become established as fact (for example the factors leading to the poor success rate of *L. cuprina* breeding in carrion).

However, questions emerging from my previous work (Williams and Richardson, 1983; Williams and Richardson, 1984; McQuillan, Jones and Williams, 1983) cast doubt on these generalisations (at least on the regional scale, that is, in Tasmania) and so warranted further work to clarify them. There were also new questions that were thought to be important in furthering the understanding of the population dynamics of *L. cuprina*,

especially in the area of phenotypic affects on the performance of adults. The present study set out to approach these problems in two broad ways.

The first was to gain better data on the species composition of the Tasmanian assemblage of necrophagous flies. As it was thought that some species such as the *Chrysomya* spp. might only be present as immigrants, a trapping program was organised to examine both the seasonal and geographic distribution of flies within Tasmania. The trapping program was also taken as an opportunity to examine the fine scale distribution of field populations, and to perform experiments aimed at determining the species emerging from carrion.

The second aim was to examine the effects of competition on *L. cuprina*. This entailed laboratory experiments on the effects of larval competition on cohorts of larvae and the ensuing adults, in simulations of each of the alternative larval habitats (*ie.* carrion and myiasis). The results of this work were extended to an examination of the field populations, and finally to a study of the effects of competition on the ability of *L. cuprina* populations to persist locally.

1.4.1 A NOTE

The field work for this study took place over two summer seasons (1982-1983, 1983-1984). Both these years fell within a long period of severe drought affecting Tasmania. Because of this it is thought that the field densities of *L. cuprina* were comparatively low and thus any comparison of the results presented here with other studies should consider this factor.

1.5 DESCRIPTION OF TERMINOLOGY USED

As there seems to be more than one acceptable nomenclature for stages of the life

history of blowflies, I shall outline the terminology used here. For the sake of compatability, this terminology is based on that used in the contemporary Australian literature.

The pre-adult subsystem starts at the **egg stage**. Eggs are laid on the food source and at hatching the ensuing larvae immediately start feeding (**trophic or feeding larvae**). Instars in the larval stage are marked by moults. The first and second larval instars are passed through in the feeding stage, however during the third instar, larvae cease feeding and leave the food source. This marks the beginning of the **wandering stage** in which larvae search for suitable pupation sites.

The wandering stage is followed by a period of voluntary immobility, and at this point larvae may enter **diapause** (retaining the ability to be mobile if adverse conditions or disturbance are experienced); or the **quiescent stage**. This stage is marked by the immobility of larvae even upon disturbance, and typically the contraction of the body into an ovoid shape. During this stage the outer skin of the larvae becomes tanned (forming the **puparium**), and the pupal respiratory apparatus is formed (pupal "horns"). It is at this point that **pupation** commences.

A **pharate adult** develops within the puparium. Pupation is completed upon the **emergence** of a **teneral adult** from the puparium. In the case of female flies, the teneral period ends with the completion of **stage 0** of the **ovarian cycle**. The adult females then continue development through several ovarian cycles (one cycle is composed of stages I through to stage V) [see Section 5.1.1]; each cycle is completed by the laying of a **batch** of mature eggs.

A diagrammatic representation of the life-cycle is given in Figure 1.1.

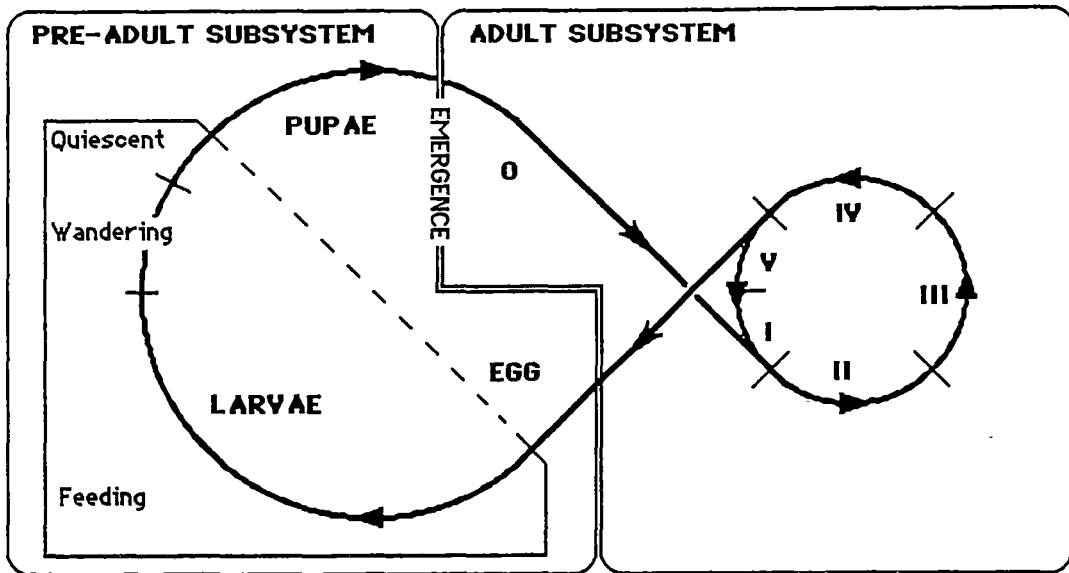


Fig 1.1 The life-cycle of *Lucilia cuprina*. Roman numerals denote egg stages defined in Sect. 5.1.1.

Glossary

blow - deposit eggs; *overblow* - deposit more eggs than the resource can support.

breech strike cutaneous myiasis of the breech area.

mulesing - removal of the skin around the breech; *radical mulesing* - removal of the skin around the breech and removal of the tail. These operations result in smooth naked scar tissue and are thus less susceptible to predisposing conditions of strike such as scalding by urine and scouring by faeces kept in contact with the skin by fouled wool.

myiasis the invasion of living tissue by larvae of Diptera; *cutaneous myiasis* - invasion of the living cutaneous tissue.....

oviposition - to lay eggs; *viviposition* - to lay live young; *ovoviviposition* - to lay live young sheathed within a persistent egg membrane.

parasitoids an organism alternately parasitic and free living.

primary, secondary and tertiary stage species of necrophagous flies (primary flies) those species which are associated with original invasion of tissues/carrion, (secondary flies) those that are found in association with primary flies and seldom as the sole species, (tertiary flies) those that are found in association with secondary flies.

CHAPTER 2.

FIELD EQUIPMENT AND PROCEDURES.

2.0 INTRODUCTION

This chapter will describe the basic field equipment and techniques used during the project. The primary aims of the field work were to determine the species of flies present, the spatial distribution of field populations, and the species breeding in carrion.

As the aim of this study was to examine the interactions of the species, the spatial distributions of the populations were of interest. Existing equipment for sampling blowfly populations [the modified W.A. bait trap described by Vogt and Havenstein (1974)] proved too clumsy and expensive for such a study, so new techniques were developed for high density trapping in a manner suitable for an appropriate statistical analysis.

2.1 TRAPPING PROCEDURES

2.1.1 DEVELOPMENT OF A NEW TRAP

2.1.1.1 Introduction

In view of the expense in the construction of the standard "West Australian" (W.A.) bait trap a new model was developed for use in the population studies. The new version used the same principle as the W.A. bait trap but took advantage of modular plastic products in fabrication.

The "West Australian" (W.A.) bait trap was originally described by Newman and Clark (1926), and standardized for population studies by Gilmour *et.al.*(1946). Improvements to the standard design were made by Vogt and Havenstein (1974). The trap is now widely used in blowfly population studies, as the only effective means of sampling flies, even though the sample is heavily biased to the phases of adult flies which are actively searching for protein.

As shown by Vogt and Havenstein (1974), the standard W.A. bait trap is expensive in both materials and construction. At current prices one trap costs approximately \$130 in materials and labour. Assuming that 10-12 replicate traps are needed for a population survey, an outlay of \$1300 minimum is required.

The trap described here uses poly vinyl chloride (P.V.C.) components produced for the plumbing trade allowing for cheapness, greater rigidity in the overall structure and ease of servicing. This design employs the same principle as the standard W.A. bait trap; however components cost approximately \$5.00 and each requires about one hour of labour to fabricate.

2.1.1.2 Materials and method of construction

The assembled trap is illustrated in Plate 2.1, with a vertical section shown in Fig. 2.1. The fly chamber is constructed from an opaque plastic 4.5 litre screw-top jar (Australian Consolidated Industries International P/L.Y23-143). Four 15 x 11cm windows are cut into the sides of the jar and glass fibre fly screening (mesh size =0.18cm) is applied over these by 'welding' the screen to the plastic with a soldering iron. A small hole (3mm diam.) drilled into the centre of the base of the jar provides an opening permitting a wire hook to pass for attaching the trap to the stand.

The cone is also constructed from glass fibre screening using a sheet metal template as a cutting guide. The cones are stapled together and held in place between the lip of the jar and the jar's lid, from which a hole of 8 cm diam. is removed. The jar's lid is cemented with P.V.C. glue to the inside of the entry chamber. Because the lid's outside diameter is less than the internal diameter of the entry chamber it is necessary to use a filler ring made from off-cuts of the piping used for the entry chamber.

The entry chamber consists of a 14cm length of Storm Water and Vent (S.W.V.) 10cm P.V.C. pipe. The jar's lid is glued into this to a depth at which the bottom lip of the lid is 1cm below the cut edge of the pipe. Ten holes of 1.6cm diam. each are drilled around the other end of the pipe with the bottom edge of the holes 2.5cm from the end (this is done so as not to obscure the holes when the push-on cap is in place).

The 10cm P.V.C. push-on caps (Hardie Iplex S38), have an 8cm centre well, which serves as a bait receptacle. A length of S.W.V. 8cm P.V.C pipe (6.4cm long) is cemented into this well.

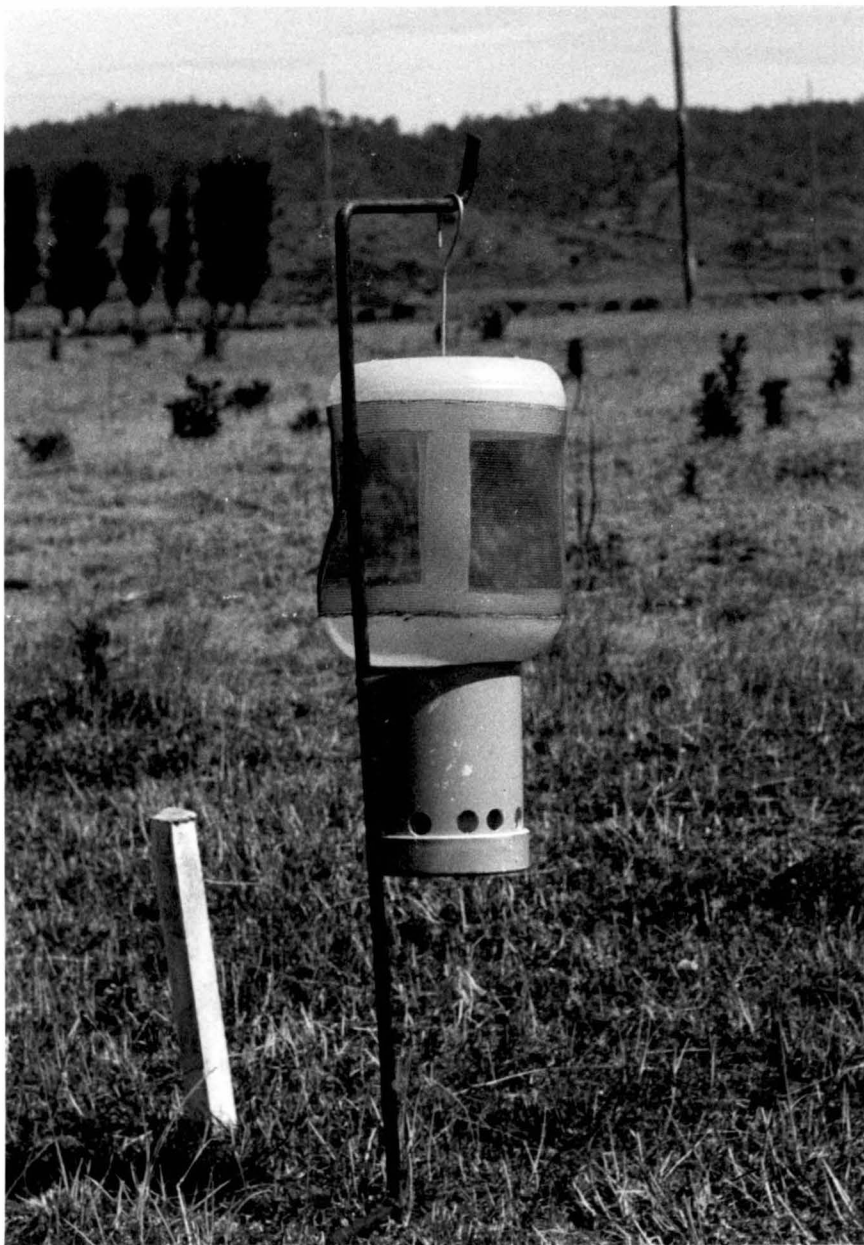


Plate 2.1. The assembled trap in the field.

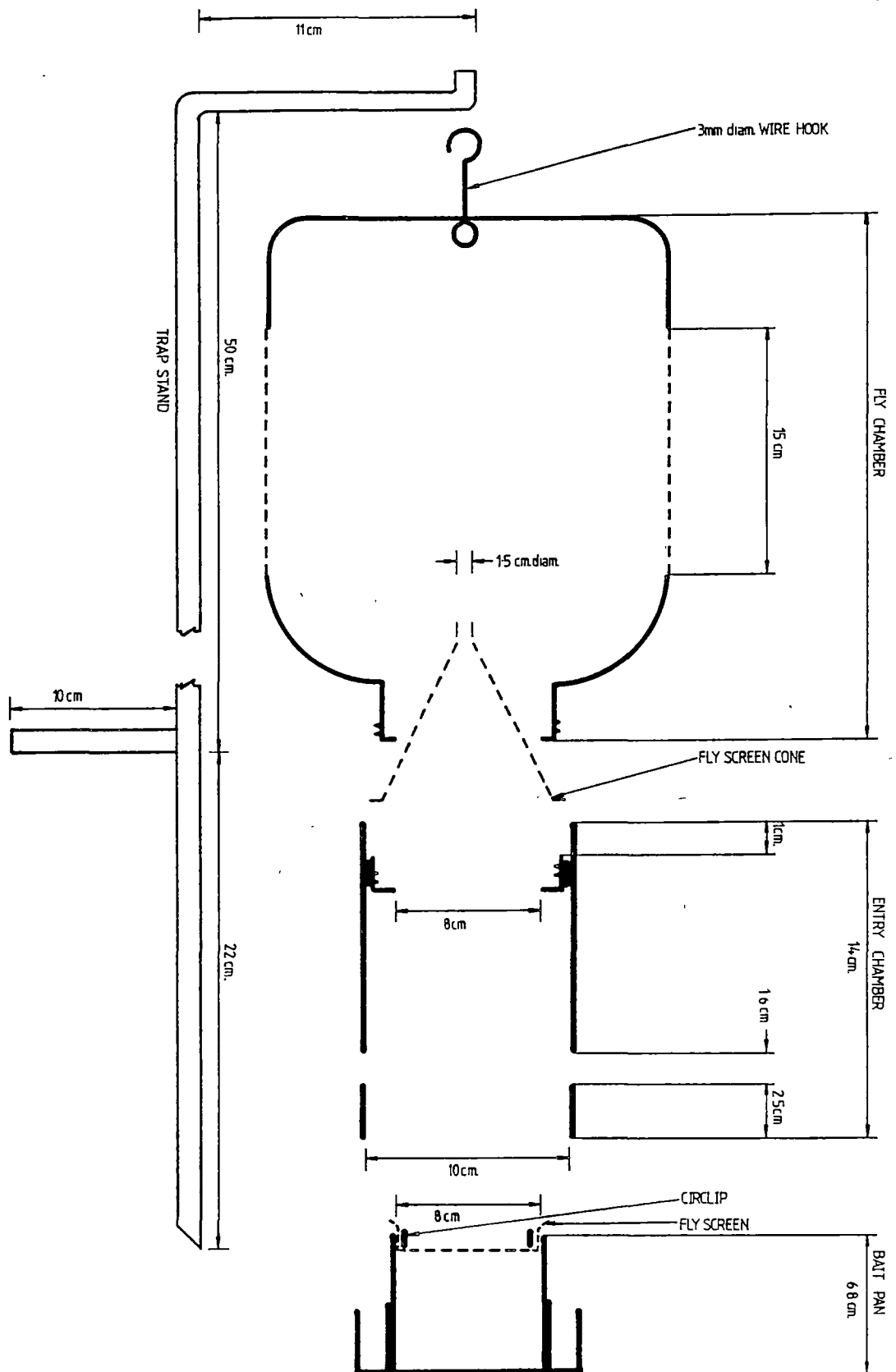


Figure 2.1. Cross section of the trap.

To exclude flies from the bait, a circle of fly screening (10cm diam.) is fixed inside the top of the bait pan using a cir-clip made from a thin off-cut of the 8cm pipe with a 3cm length cut from its wall. Fixing fly wire over the top of the bait pan with a rubber band or similar device is not recommended as this reduces the clearance between the entry holes and the bait pan's sides (which is approximately 1.6cm) and thus may hamper the flies' access to the main body of the entry chamber.

The trap is hung by the hook at the top of the fly chamber from a stand made of 10mm black round steel. The stand is 72cm in length, with a cross-piece welded on at 22cm from the angle cut end acting as both a convenient means of inserting the end into hard ground and a spacer ensuring that the arm at the top will be 50cm above the ground. The arm is 18cm in length including the upturned end, so starting with a piece of steel 90cm long the arm is easily bent from this. A rubber band can be put around the stand and entry chamber to prevent the trap from swinging in the wind.

The bait pan and entry chamber are painted yellow to increase the attractiveness of the trap to blowflies, in a manner similar to the standard W.A. bait trap. The new model is baited with the same bait as specified for the standard W.A. bait trap (Vogt and Havenstein 1974). However the volume of the bait is reduced from 1.5kg liver and 1 litre sodium sulphide solution (standard W.A. bait trap), to 50-60g liver and 30ml sodium sulphide solution (new model). The sodium sulphide solution enhances and prolongs the attractiveness of the bait to primary blowflies and is prepared by adding 20g crystalline sodium sulphide to 1 litre water (Vogt and Havenstein, 1974).

2.1.2 THE STICKY TRAP

As an alternative type of trap, and to get higher trap densities, 'sticky traps' were

also constructed. The trap design was copied from those used by the CSIRO Division of Entomology, (Wardhaugh *et al.*, 1983a).

2.1.2.1 Materials and method of construction

The trap consisted of a square of fibro-cement board 16cm x 16cm with a 2.5cm diameter hole drilled in the centre. The board was then covered with a commercially available insect adhesive (Tanglefoot®), leaving a 1 cm strip around the edge free of adhesive for easier handling. The hole in the middle of the board held the bait receptacle, which consisted of a small plastic cup filled with minced liver and the sodium sulfide solution described above. The lip of the cup was level with the board when inserted.

2.2 RESULTS AND DISCUSSION

2.2.1 THE NEW TRAP

2.2.1.1 General performance of the new trap

The traps were used throughout this project from the summer trapping program of 1982-83 to the 1984-85 season. Over approximately 3800 trap hours of operation minor repairs were required only twice. The new trap model required 5 minutes to open and 10 minutes to close (time for killing and bottling flies included).

No interference by ants was experienced in the operation of the new model, however if ants should pose a problem the practice of applying grease at the base of the stand should be satisfactory in blocking access to the trap.

2.2.1.2 Calibration to the Standard W.A. bait-trap

For the purposes of calibration, a field trial was conducted on 4/3/83 to compare the new trap with the standardised W.A. bait trap. Two adjacent trapping grids were established on a sheep farm at Powranna in central Tasmania, with 7 standard W.A. bait traps on one grid and 10 of the new model on the other (see Sect. 3.1.2.1 for a description of the trapping grids). The two types of traps were opened and closed simultaneously at 0900 h and 1700 h respectively. All *Lucilia* spp. and *Calliphora* spp. were counted and the mean catch per trap is given in Table 2.1.

Trap model	<i>L. cuprina</i>	Mean number caught per trap				Number of traps	Bait used per trap	
		<i>L. sericata</i>	<i>C. stygia</i>	<i>C. hilli</i>			Liver (g)	Na ₂ S solution (ml)
W.A. bait trap	135.4	174.0	9.3	9.8	7		1500	1000
New design	42.1	17.1	16.4	2.4	10		50-60	30

Table 2.1. Catch comparison of the modified and standard W.A. bait traps.

The new trap caught approximately 0.33 x *L. cuprina*, 0.1 x *Lucilia sericata*, 1.7 x *Calliphora stygia*, and 0.25 x *Calliphora hilli*; compared to the W.A. bait trap. Considering the reduction in bait mass (3% that of the W.A. bait trap) the new trap is more bait/catch effective.

2.2.2 THE STICKY TRAP

With the baits made up in the laboratory, the traps had a very short handling time in comparison to the more conventional traps. About 60 of the sticky traps could be deployed or collected within an hour in the field.

Originally 121 of the traps were constructed, but after trials in the field (at the main study site at Ross) only 64 were used so that only one hour would elapse from the setting of the first trap to the last. This was to minimise any variation in trap effectiveness emerging from discrepancies in opening time.

Over six trapping days or 3072 trap hours, a total of 16 flies (of all species) were caught. Apart from the extremely low apparent attractiveness of the traps the specimens caught were also dessicated and so useless for further work. The poor catch rate in comparison to that of the same traps in other studies (eg. Wardhaugh *et al.*, 1983b) is probably related to the effect of the drought in drastically reducing fly densities in the area the traps were tried. Further work with these traps was abandoned.

2.3 CONCLUSIONS

- (i). The new trap was effective for high density trapping, having a low handling time and efficient bait/catch ratio.

- (ii). The sticky trap was inappropriate for local conditions and the flies caught unsuitable for the analysis required.

CHAPTER 3

SEASONAL AND SPATIAL DISTRIBUTIONS

3.0 INTRODUCTION

This chapter examines the gross geographic distribution of necrophagous flies in Tasmania generally and the finer scale distribution of *L. cuprina* and *L. sericata* specifically. Little work is available on the Tasmanian blowfly fauna, and that which does exist, [notably Ryan (1954)] seeks to apply the factors diminishing the success of *L. cuprina* in carrion identified on the Australian mainland, to the local scene. This rationale has been questioned on several grounds by recent work.

Firstly, Williams and Richardson, (1983) have shown that in the absence of *Ch. rufifacies*, *L. cuprina* is the best adapted member of the necrophagous fly guild in Tasmania to exploit carrion based on comparisons of the flies ability to tolerate high temperatures and cope with strong inter- and intra-specific competition from native and introduced *Calliphora* spp. Secondly, McQuillan, Jones and Williams, (1983) have found that *Ch. rufifacies* is absent in Tasmania during significant periods of the seasonal distribution of *L. cuprina*. Both of these points suggest that the key factors acting against *L. cuprina* in carrion on the mainland, are not present at all times in Tasmania.

If these factors have a reduced effect in Tasmania, then it is likely that the breeding success of *L. cuprina* in carrion is higher. Norris (1959), suggested that regional population of *L. cuprina* on the Australian mainland may persist through breeding in carrion in the absence of myiasis. This proposition may be more prevalent in Tasmania.

Of principal importance to a reassessment of the interaction of the fly guild are the occurrence and role of *Chrysomya* spp. in Tasmania and the distribution and abundance of *L. sericata*. Thus a survey of representative areas of the state was required to assess the nature of the field populations before any other work could be initiated.

Sampling was designed to give information on the spatial distribution of flies. Autocorrelation analysis was then used to determine the nature and significance of any intra- and inter-specific interaction. This analysis was extended to include possible spatial interaction with sheep in the sampling area.

The analysis of fine scale structure of populations, is a comparatively recent technique. The basic approach of spatial autocorrelation with regard to biological problems was first outlined by Sokal and Oden (1978a and b), and elaborated by Cormack and Ord (1979). The analysis is based on the spatial distribution of individuals and so is quite different to that of normal dispersion indices. That is, rather than describing variance in a pattern, they distinguish the spatial location of variates.

Spatial autocorrelation provides measures of interaction between neighbouring spatial sites, measured against a random spatial arrangement. The technique has been extended by Sokal and Oden (1978a) to produce spatial correlograms which show the autocorrelation coefficient as a function of distance between pairs of localities. Correlograms summarize the patterns of geographic variation on a response surface, and interpretation of the correlograms relies in part on subjective criteria. In this chapter the analysis is used to produce correlograms describing the relationship of within species distribution, and then to the relationship of this distribution to that of other species.

This chapter also describes experiments with carrion which were done to assess the species involved, and their success during different seasons and competitive regimes (ie. the other species present).

3.1 METHODS

3.1.1 SEASONAL AND GEOGRAPHIC DISTRIBUTION

3.1.1.1 The north-south transect

In the early stages of this project a general survey of the species present in Tasmania and their spatial distribution was conducted. To this end five sites along an approximately north-south line, separated by approximately 50 km were selected in the major sheep farming areas. The sites ran along a line extending from Hobart, through the Tasmanian midlands and ending close to the north coast. They are shown in Figure 3.1.

Some means of standardising trapping effort was required to make comparisons between the various regions of the state more valid. To remove bias and maintain uniformity between sites a grid was surveyed on the most homogeneous part of sheep grazing land available at each site. The type of grid and the trapping regime used are described in Sect. 3.1.2.1. Trapping was conducted throughout the spring and summer and early autumn of 1982-83.

3.1.1.2 The major study area

After the surveys carried out in 1982-83 (see above), further field work in relation to the fine scale distribution of species, was restricted to the site at "Chiswick", Ross. The reasons for selection of this site were based on the uniformity of the land, and the temporal distribution of species. Field work at this site continued through the summer of 1983-84, and 1984-85. During this time several trapping grids were tried for various experiments and statistical analyses. These are outlined below.

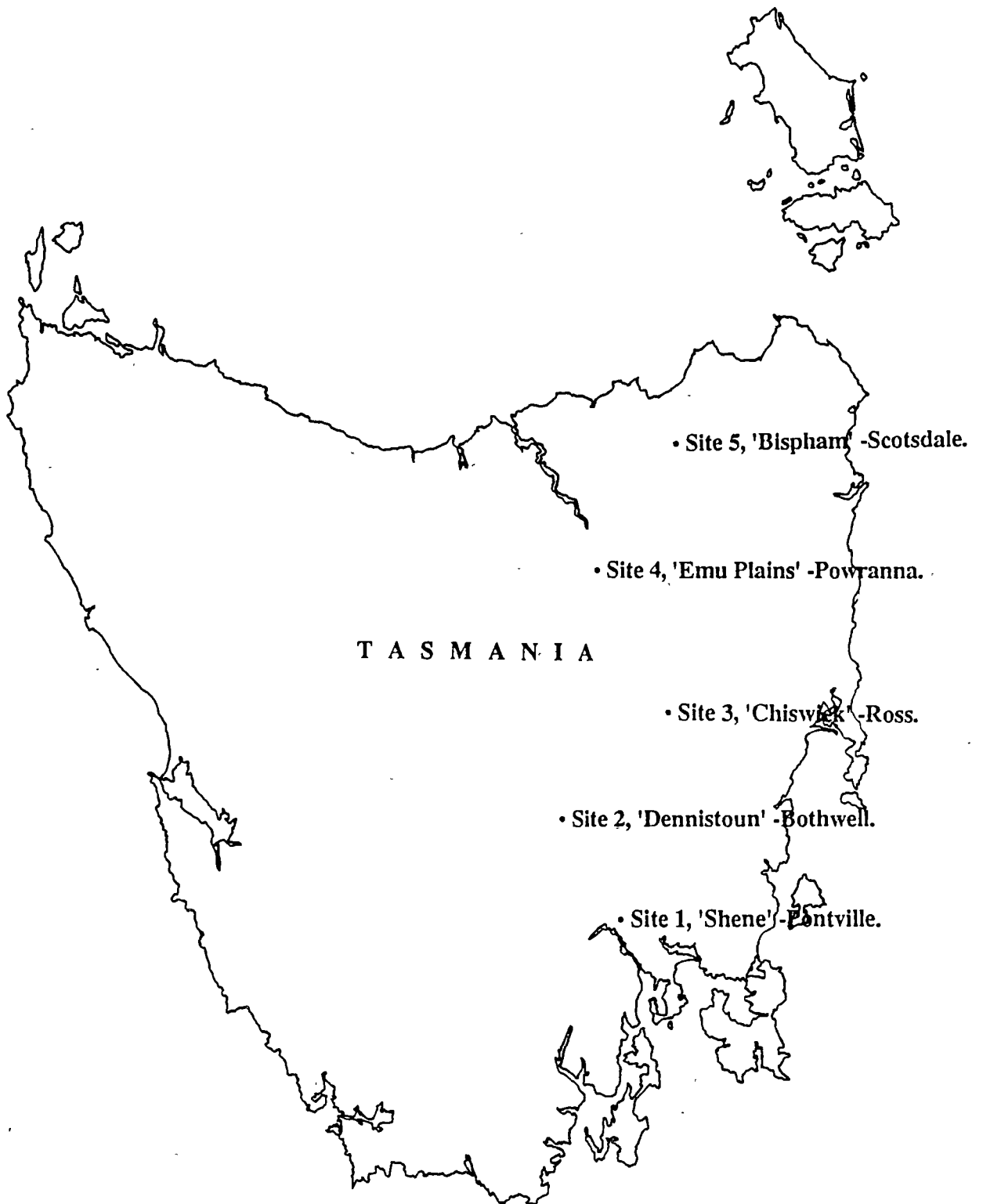


Figure 3.1. Location of trapping grids on the north-south transect.

3.1.2 FINE-SCALE DISTRIBUTION

3.1.2.1 Trapping grids

a. Stratified random sampling

Grids for stratified random sampling were used in the initial survey of species occurrence and annual abundance. The grids were 1 km by 1 km with pegs at 250m intervals. This resulted in a 5 x 5 cell grid, each cell being 6.25 hectares (ie. 250 m x 250 m) with the peg marking the centre of the cell. The pegs were labelled from 1-25. Ten traps of the modified W.A. type described above were distributed on this grid by randomly selecting cells using a standard random number generator.

The traps were set and opened at 0900 hr, taking approximately one hour to complete the operation. At the end of the day the traps were collected in the order in which they were set, starting at 1700 hr.

b. Regular lattice designs

After the initial survey, the examination of the fine scale distribution of flies within the grid became a prime objective. To this end stratified random sampling was not suitable given the statistical analyses involved. A more desirable course was to sample each cell of the grid on each trapping day. To accommodate this change in sampling a compromise had to be reached between the length of time taken to set the traps and the number of cells in the grid. This was necessary to minimise the difference in opening time of the first trap to that of the last trap.

Increasing the number of cells sampled meant reducing the handling time of each trap, and for this reason the sticky traps described in Chapter 2 were built.

The grid used with the sticky traps was originally 1 km x 1 km. Pegs were at 100

m intervals resulting in an 11 x 11 cell grid, with each cell being 1 hectare in volume. The 121 traps used on the grid took over two hours for both opening and closing. In the interest of maximising the validity of comparison between traps this time was reduced by reducing the proportion of the grid sampled. This was done by using an 8 x 8 subset of the original grid.

Even with this restriction the sticky traps did not perform satisfactorily under the prevailing conditions, and so their use was abandoned and sampling fell back on the modified W.A. bait trap.

Using the modified W.A. bait traps with the regular lattice sampling meant again reducing the number of cells in the grid, as the handling time of these traps was greater. To accommodate this the number of cells in the second sticky trap grid were reduced by amalgamating adjacent cells to give a 4 x 4 cell grid. The pegs were then 200 m apart and the cells had an area of 4 hectares. Figure 3.2 presents the location of all trapping sites for each grid on "Chiswick".

3.1.2.2 Analysis of the trap data

a. Stratified random sampling on the N-S transect.

The catch from each day's sampling at each site was segregated by species and sex. Seasonal abundance was determined by plotting against date the mean number of a species (males and females) at a site (ie. the mean catch of all the traps set on a sampling day).

Species abundance on the grid was principally made by visual inspection of the data. Plots were made of the raw data using the 3-dimensional contour plotting routine SURFACE 2. Plots by day, site, and species were generated by this method. To describe

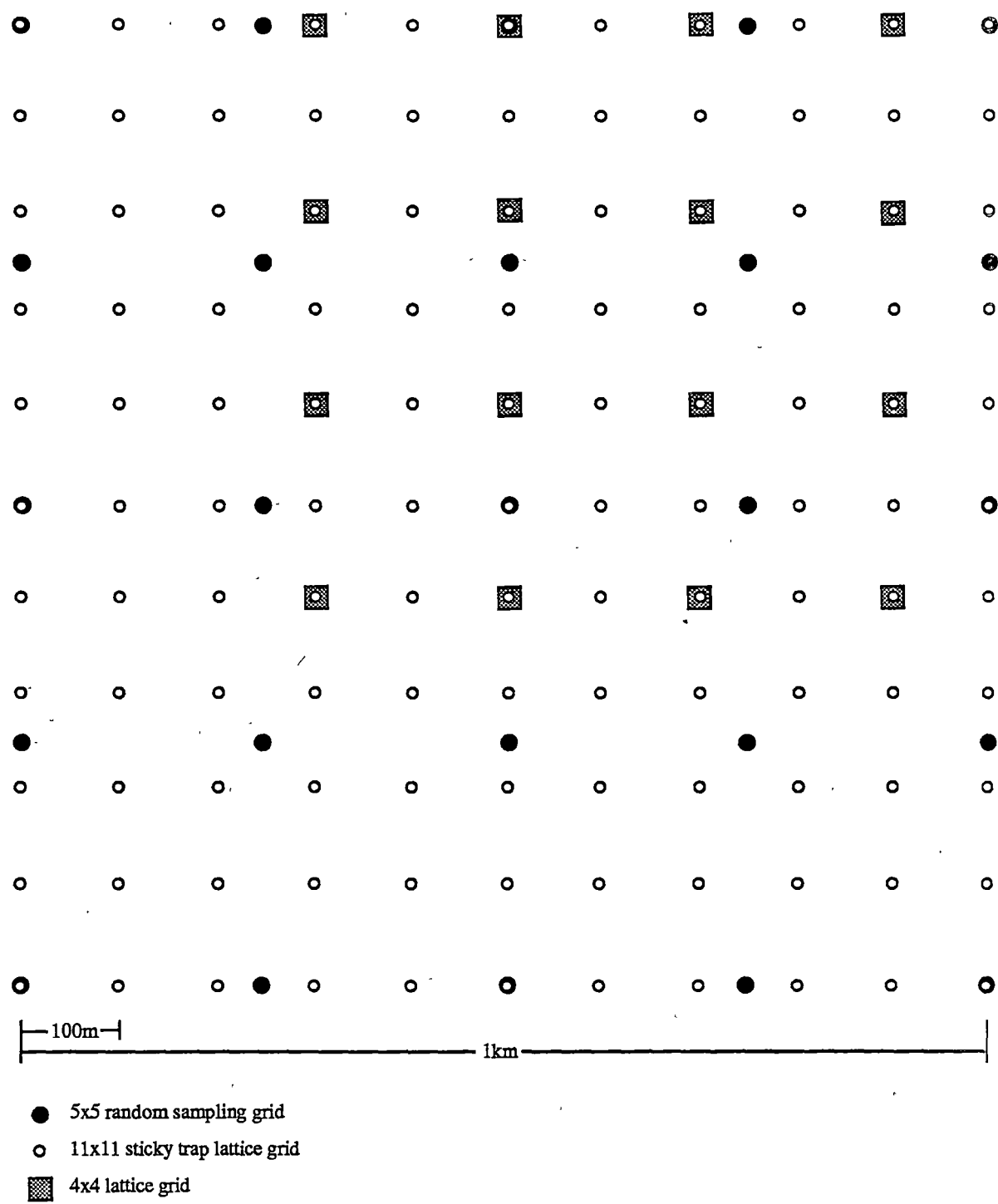


Figure 3.2. The relative locations of trap sites on the three grid patterns used at Site 3, 'Chiswick'.

the fundamental dispersion pattern of each species a dispersion of means index, (I_{DM}) was used. The index is calculated as follows.

$$I_{DM} = \left(\frac{s^2}{m} \right) - 1$$

where I_{DM} = dispersion of means index,

m = the mean species abundance from traps at a site,

s^2 = the between trap variance of species abundance at a site,

Values of I_{DM} are in the range $-\infty$ to $+\infty$. As a rule-of-thumb the values of I_{DM} can be interpreted as showing-

$I_{DM} = 0$, for random distributions with $s^2 = m$.

$I_{DM} > 0$, for contagious distributions with $s^2 > m$.

$I_{DM} < 0$, for regular distributions with $s^2 < m$.

This analysis only generates an index of the dispersion pattern of a species as a whole and so ignores the spatial organization of the data, it is also not possible with this analysis to examine the spatial interaction between species. To enable an analytical approach which would account for spatial structure, the grid sampling was changed and is described below.

b). Regular lattice trap data.

Once again for visual inspection the SURFACE 2 package was used to generate contour plots of abundance on the trapping grid. The analysis used was spatial autocorrelation. This technique generates coefficients of spatial autocorrelation between samples, and accounts for the position and distance of the samples from each other. The techniques as applied to biological populations are described by Jumars et al., (1977) and Sokal and Oden (1978a,b). The analysis for spatial dependence of variates from point sampling on a regular lattice is given below in two parts. The first deals with the analysis of intra-specific autocorrelation and the later, inter-specific.

1). Intra-specific autocorrelation [after Ord (1979)] .

Given cells in a lattice that are labeled $1, 2, \dots, n$; let y_i be the value of y in the i^{th} cell ($i=1, \dots, n$).

Now $E(y_i) = m$, $\text{Var}(y_i) = s^2$ and $\text{Cov}(y_i, y_j) = s^2 r_{ij}$.

where r_{ij} is the autocorrelation and depends on the relative position of sites i and j .

Taking into account the distance (or any weighting between the sites) the representation is,

$r_{ij} = r(\partial_{ij})$ where ∂_{ij} is the distance or weight between sites i and j and $r(\partial_{ij})$ is the spatial autocorrelation function.

Weighting in this case was taken as the distance between cells in grid units. The pattern of cells considered (j) around cell i is given in Figure 3.3.

The test statistic used is Moran's coefficient of spatial autocorrelation (I_{Mc}). It takes the form,

$$I_{Mc} = n \frac{\sum_{(2)} (\partial_{ij} z_i z_j) / \sum_{(2)} \partial_{ij} \sum_{(1)} z_i^2}$$

Where $z_i = y_i - Y$ (Y is the mean y_i of all cells),

The summation notation used is,

$$\sum_{(1)} = \sum_{i=1}^n, \text{ and } \sum_{(2)} = \sum_{i=1}^n \sum_{j=1, i \neq j}^n$$

The significance of I_{Mc} can be tested by treating I_{Mc} as a standard normal deviate under two models of the distribution of I_{Mc} . These are as follows.

i). Assumption N: that y_1, \dots, y_n are independent and identically distributed normal random variables with,

$$E_N(I_{Mc}) = -(n-1)^{-1}$$

$$\text{and } E_N(I_{Mc}^2) = (n^2 S_1 - n S_2 + 3 S_0) / [(n^2 - 1) S_0^2]$$

$$\text{where } S_0 = \sum_{(2)} \partial_{ij}$$

$$S_1 = 0.5 \sum_{(2)} (\partial_{ij} + \partial_{ji})^2$$

$$S_2 = \sum_{(1)} \left(\sum_{(3)} \partial_{ij} + \sum_{(3)} \partial_{ji} \right)^2$$

where $\sum_{(3)} = \sum_{j=1}^n$

ii). Assumption R: the distribution of I_{Mc} is based upon the set of all possible random permutations of y_i around the n sites.

$$E_R(I_{Mc}) = E_N(I_{Mc})$$

$$E_R(I_{Mc}^2) = n[(n^2-3n+3)S_1 - nS_2 + 3S_0^2] - b[(n^2-n)S_1 - 2nS_2 + 6S_0^2] / (n-1)(n-2)(n-3)S_0^2$$

$$\text{where } b = \sum_{(1)} z_i^4 / (\sum_{(1)} z_i^2)^2.$$

Cliff and Ord (1973) demonstrate that the distribution of I_{Mc} approaches normality with increasing n , provided that ∂_{ij} is a positive real number.

2). Inter-specific autocorrelation [after Kooijman (1979)]:

For species that may differ from each other the Moran statistic can be generalised to-

$$I_{Mc}(a,b;W) = (ab)^{-1/2} y_a' W y_b (1' W 1)^{-1}$$

using standard matrix notation,

where y_x' is the scalar vector of centered cell contents of species x present on the grid.

a and b are the variance of cell contents for species a and b respectively).

W is the weighting matrix as described above, and the cell contents are centered such that $E y_a = 0$.

1 is the vector of length n and defines the matrix multiplication, while n is the number of cells.

I_{Mc} can be tested under the same models discussed above. For both assumption R and N,

cell contents are centered so that $E(y_a) = E(y_b) = 0$.

Thus with $E(I_{Mc}) = 0$

$$E_R(I_{Mc}^2) = (1 / w_{++}^2) \{ [n^2/(n-1)^2] \sum_{(2)} \partial_{ij}^2 - [n/(n-1)^2] \\ [\sum_{(1)} \partial_i^2 + \sum_{(3)} \partial_j^2] + [1/(n-1)^2] w_{++}^2 \}$$

and $E_N(I_{Mc}^2) = \sum_{(2)} \partial_{ij}^2 / w_{++}^2$

In all cases when evaluating the standard normal deviates $E_R(I_{Mc})$ and $E_N(I_{Mc})$ the significance levels are,

$$P \leq 0.1 \quad [10\%], \quad |E(I_{Mc})| \geq 1.644$$

$$P \leq 0.05 \quad [5\%], \quad |E(I_{Mc})| \geq 1.960$$

$$P \leq 0.01 \quad [1\%], \quad |E(I_{Mc})| \geq 2.580$$

For the analysis of intra-specific distribution patterns a FORTRAN IV program ACORN was jointly developed with I. Woodward of the Zoology Department, University of Tasmania. The analysis of inter-specific distributions used a FORTRAN IV program WALNUT, developed by I. Woodward.

The data for this analysis were in three forms. The first form was from the stratified random sampling data. For the purpose of this analysis, cells of the 5 x 5 grid not sampled (15) were treated as missing values. The second form was simply of cell counts (ie. trap catches of fly species) per trapping day for the flies in the regular lattice sampling program. For the analysis of inter-specific autocorrelation a third form was used to quantify the distribution of sheep within the trapping grid.

The location of sheep flocks in the grid was mapped on an hourly basis during trapping. Each cell was then scored for the size of flocks, their proximity to the trap, and the duration of the pattern through the day by using the overlay shown in Figure 3.4. The

overlay was placed over a cell and the number of segments more than 50% occupied by sheep counted. This was repeated for each cell and hourly map, and finally the cell scores by hour were summed for the whole day.

It can be seen from Figure 3.4 that segments are distance weighted. A bias is introduced by making the area of a segment to be occupied before being counted increase with increasing distance from the trap. This was seen as the simplest model that could be used to equalise the catch of flies in a trap (as an index of fly abundance) to the distribution of sheep as an index of sheep abundance. In effect it assumes that the influence of the trap within in a cell conforms to the inverse square law.

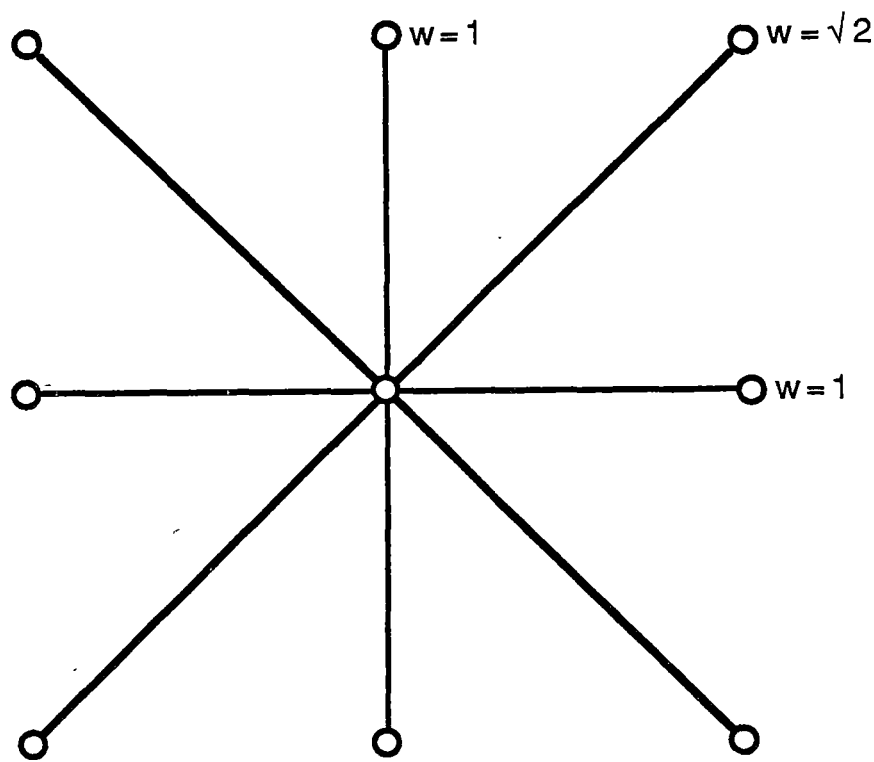


Figure 3.3. Weighting constants used for autocorrelation. The central circle represents the trap cell i,j , the other circles being its possible neighbours in the lattice.

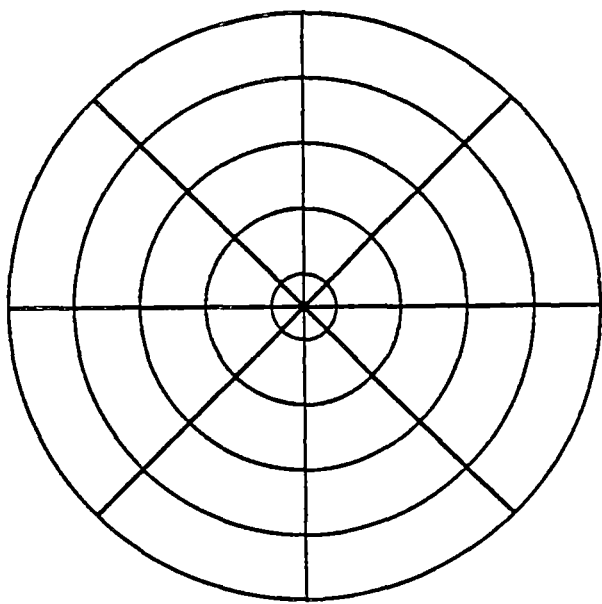


Figure 3.4. Overlay used for calculating the index of sheep abundance in a trap cell. The diameter is 200m.

3.1.3 CARRION EXPERIMENTS

3.1.3.1 Introduction

Most equipment designed to assess the species involved in carrion interferes with the natural sequence of events occurring in a carcass (Norris, 1965). Because of this the outcomes of succession and interaction between the species present are biased resulting in outcomes which are not realistic. For instance, Waterhouse (1947) found that rims on larval collecting trays placed under a carcass favoured *Chrysomya rufifacies*.

Larvae of most species of blowfly wander some distance from the carcass before pupating. *Calliphora stygia* may wander 5-6 m from a carcass, whilst Vogt and Woodburn (1982), found that *L. cuprina* larvae had a median dispersal distance of up to 1.6 m from a carcass. A major objective of the carcass experiments in this project was to determine whether or not *L. cuprina* was present in carrion. Thus, it was not necessary to recover representative samples of all flies present, but rather to optimise the recovery of *L. cuprina*, without disturbing the carcass and thus affecting the normal outcome of competition.

With this objective in mind, emergence tents which could be placed over the carcass after the last primary maggots had left were constructed. The area of ground covered around the carcass was maximised to capture as many emerging *L. cuprina* as possible. Two experiments were run, one with carcasses exposed when *Ch. rufifacies* was present and the other earlier in summer when *Ch. rufifacies* was absent.

3.1.3.2 Competition in the presence of *Chrysomya* (Emergence tent Type 1)

For the 1983-84 summer season, three emergence tents with solid steel aprons and covering 2.56 m² of ground were constructed. The apron consisted of four 1.6 m lengths of 3 cm channel section steel welded into a square. To this base was attached a fibreglass

flyscreening square section cone, of 1 m height. The cone terminated in a circular metal sleeve, of a diameter which would fit tightly around the fly chamber/entry cone section of a modified W.A. bait trap (approx. 10cm diam.). The cone was supported by steel rods secured at the corners of the apron and to the metal sleeve. They could be removed to collapse the apparatus during transportation.

The carrion experiment using this type of emergence tents were started at the 'Chiswick' site after the first appearance of *Ch. rufifacies* in the trapping program for that year (early March). Sites for the carcasses were selected by the nature of a cells trapping record on the grid prior to March. The three sites were selected on the grounds of highest mean *L. cuprina* (alone) catch, highest mean *L. sericata* (alone) catch, and highest *L. cuprina* and *L. sericata* (combined) catch. These were sites 9, 4 and 15 respectively (see Figures 3.7 a and b).

The carcasses used were those of three freshly slaughtered Polworth 4-tooth wethers. The sheep had four months of fleece, similar condition (they were from the same flock) and were killed on the site by shooting in the head. The carcass placed at the site selected for the abundance of *L. cuprina* was also used to examine temperature history through succession. (See Section 3.1.3.3).

Carcasses were observed at intervals of two days, and when the primary fly maggots had left the corpse an emergence tent was placed over it. The fly chambers were emptied on a weekly basis after the first emergence of flies. Collecting the sample was simply a matter of removing the fly chamber/entry cone section and replacing it with another empty one. The flies were then killed with a pyrethrin spray and removed to storage in alcohol, with no losses from the sample.

3.1.3.3 Competition in the absence of *Chrysomya* (Emergence tent Type 2)

In the 1984-85 summer season, an alternative emergence tent design was used which covered a greater area of ground. These tents had a cloth apron with grommets so that they could be pegged in place. The sides were 3.5 m in length and the ground coverage was 12.25 m². The cone was constructed of the same material as the Type 1 emergence tents, and had the same fitting to take the fly chamber. Support for the cone and fly chamber was by a steel rod welded to the circular metal sleeve which could be driven into the ground next to the carcass supporting the fly chamber 2 m above it. Pictures of the assembled emergence tents are given in Plates 3.1 a, b.

Carcasses for this season were exposed in January, a time at which *Ch. rufifacies* was known to be absent from the area. The absence of *Ch. rufifacies* during the time the carcasses were exposed was confirmed from the trap data. The sites selected for this season (1984-85) were based on the same selection criteria as described in Section 3.1.3.2. The methods followed and the type of carcass used were also the same as for the previous experiment.

3.1.3.4 Temperature history of the carcass

During the first series of carcass experiments, the temperature history of a carcass was measured during the initial successional stages of decomposition. Temperatures were measured using seventeen thermistor probes introduced to different parts of the carcass, and an additional probe was used to measure the ambient air temperature. Thermistors used were of the Grant OR4 type, and temperature was recorded at twelve hourly intervals by a Grant Model D recorder. The position of the probes is shown diagrammatically in Figure 3.5. The probe measuring ambient air temperature was located in a Stevenson Screen next to the carcass.

The carcass chosen for this work was that allocated to the position of greatest

mean *L. cuprina* abundance. This carcass was selected since the primary objective of this experiment was to see if temperature was a major factor determining the outcome of interaction between *L. cuprina* and *Ch. rufifacies* . Temperature recordings were recorded for the first twelve days after the carcass was placed in the field.



Plate 3.1 a. The Type 1 emergence tent assembled in the field.



Plate 3.1 b. The Type 2 emergence tent assembled in the field.

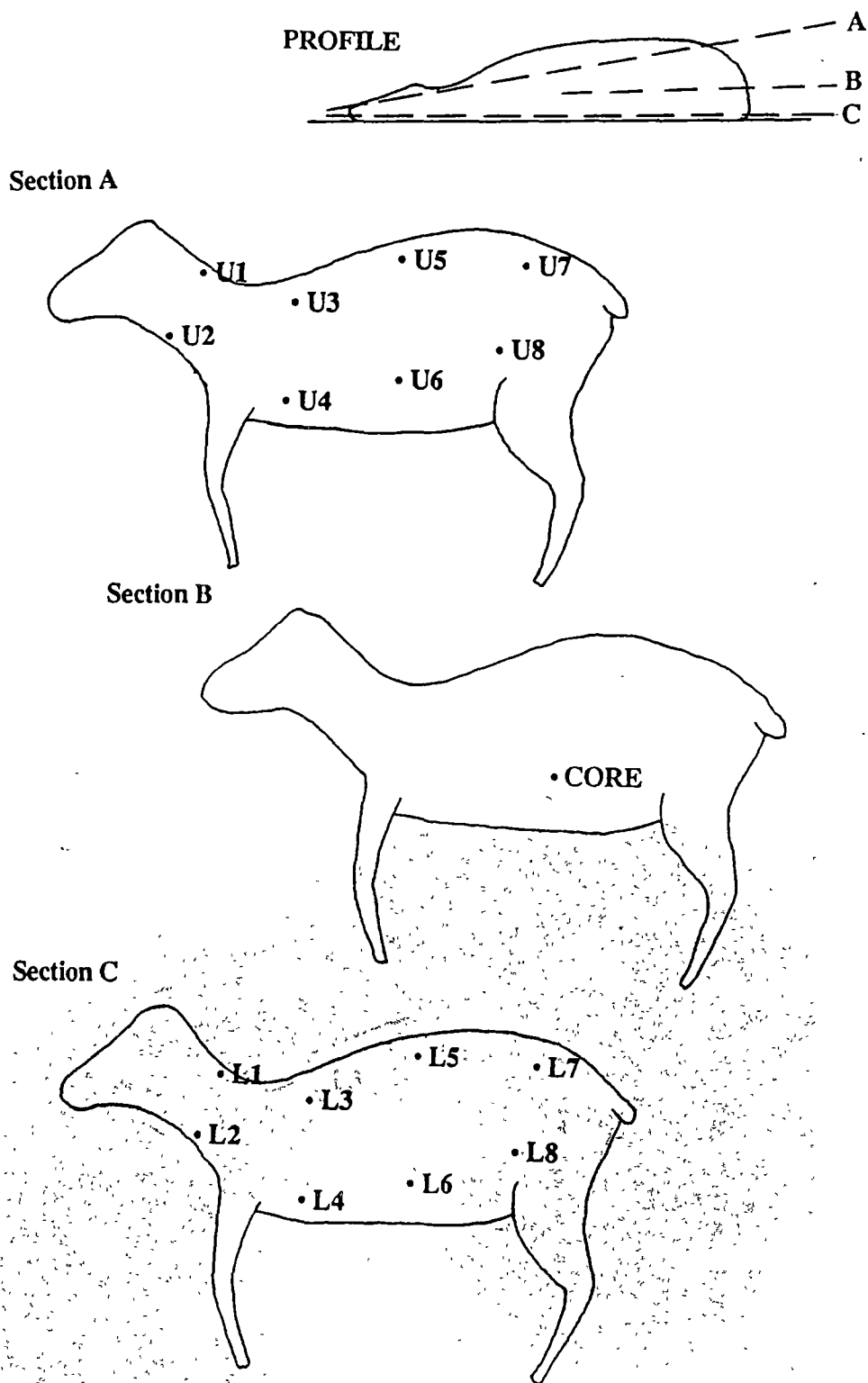


Figure 3.5. Location of the temperature probes within the sheep carcass. Horizontal sections refer to the profile given above.

3.2 RESULTS

3.2.1 SEASONAL AND GEOGRAPHIC DISTRIBUTION

The abundance of fly species at the five sites on the north - south transect are given in Figures 3.6 (a-e). Small and occasional catches were made of flies from the Sarcophagidae, Fanninae and Muscidae. These are not reported here as their occurrence is incidental and of little importance to the necrophagous fly guild.

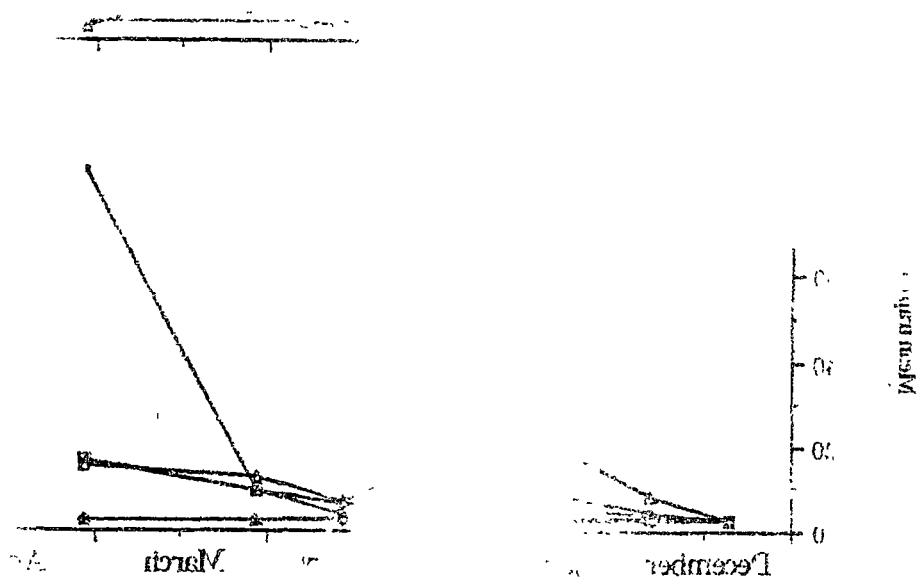
Compared with the abundance of *L. cuprina*, *L. sericata* and *C. stygia* the contribution of *C. hilli* and *C. vicina* to trap catches are minor. Whilst the species mentioned above occurred at all of the trap sites and were present throughout the trapping program, the occurrences of *Ch. rufifacies* and *Ch. varipes* are limited.

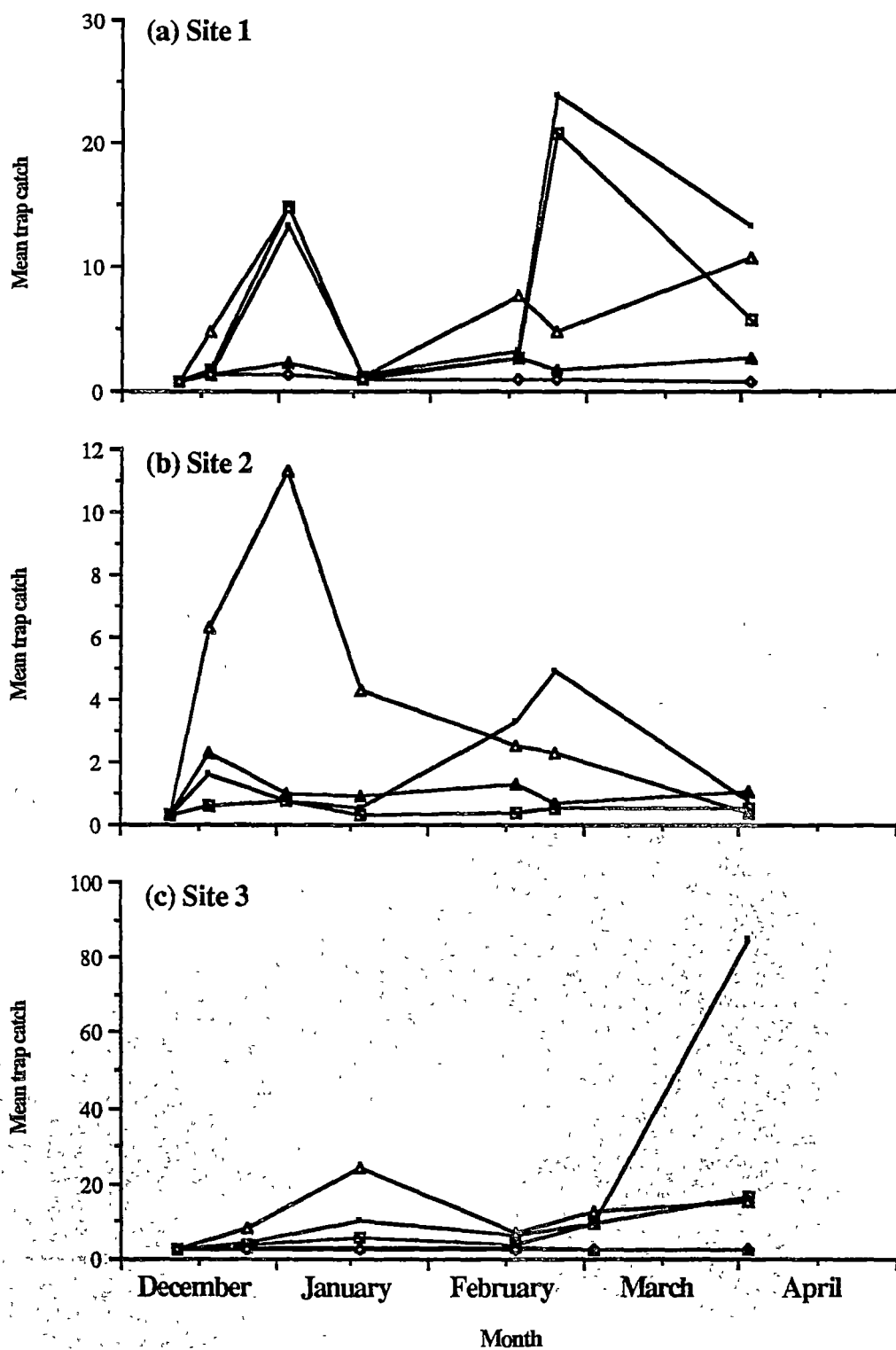
Ch. varipes is restricted to the most northerly site and it is present for the same period as *Ch. rufifacies* at this location. The distribution of *Ch. rufifacies* is interesting when the date of its first occurrence and the location are considered. Thus the first occurrence of *Ch. rufifacies* is later in proportion to the distance south on the transect. *Ch. rufifacies* was not caught at sites south of Ross in the trapping program.

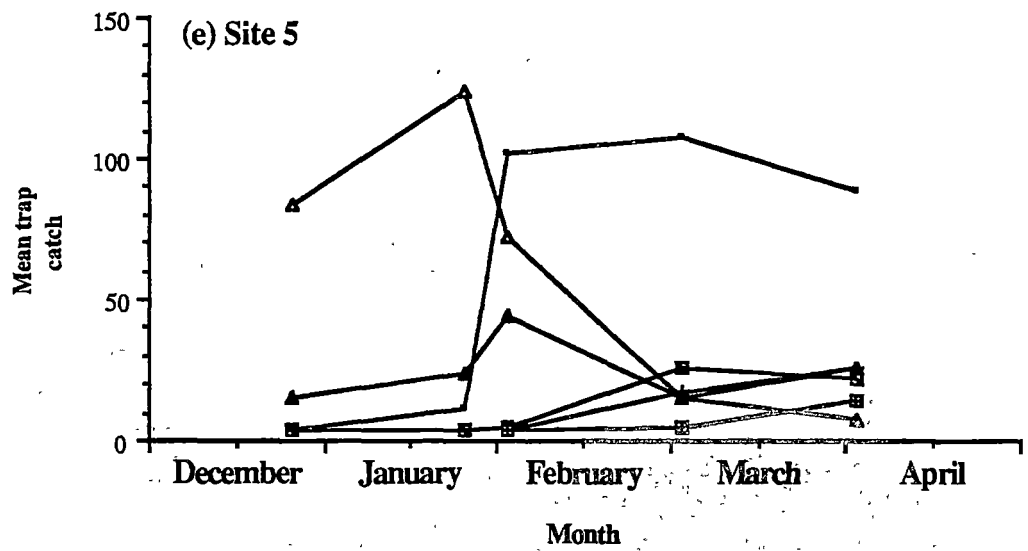
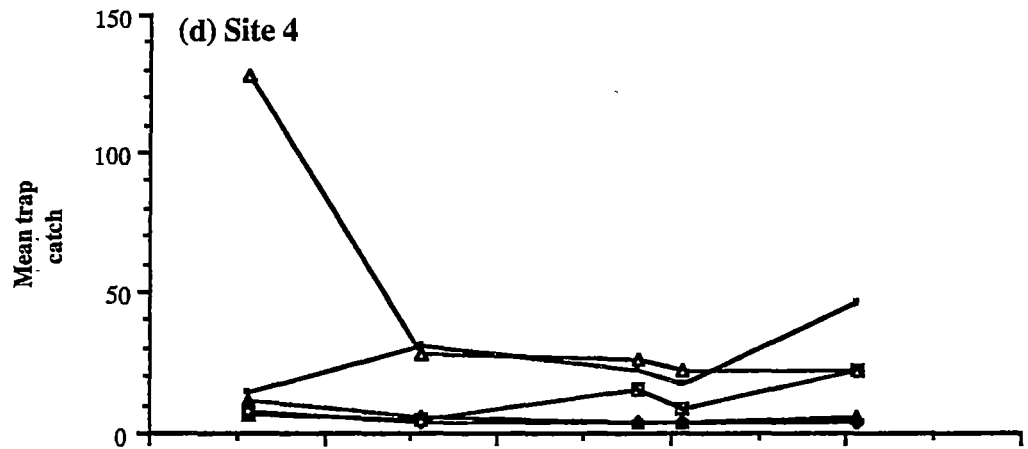
General trends in the seasonal abundance of flies at the trap sites are as follows.

- i) *L. cuprina* is most abundant in late February through to early April when trapping was terminated. There is no obvious change in abundance for *L. sericata* except at site 1 where abundance peaks in January.
- ii) the numbers of *C. stygia* peaks during November and December.
- iii) *C. hilli* and *C. vicina* remain at constant but low levels at all sites except the most northerly one where *C. hilli* forms a more significant proportion of the catch.
- iv) the numbers of *Chrysomya* spp. increase from the time of first capture to the end of the trapping program.
- v) at all sites *L. sericata* forms a significant portion of the catch.

Figure 3.6. Abundance of flies in mean per trap for all sites on the north-south transect.







- L.cuprina
- L.sericata
- C.stygia
- C.hilli
- C.vicina
- Ch.rufifacies
- Ch.varipes

3.2.2 FINE-SCALE DISTRIBUTION

3.2.2.1 Intra-specific effects

a). Stratified random sampling.

Values of the dispersion of means index (I_{DM}) for trapping days in the 1982-83 season are given in Table 3.1(a-e) by trapping day and species. As has been discussed earlier this analysis does not account for the effects of the position of traps in relation to each other. The index describes the gross distribution of abundance from randomly distributed sampling sites. From Table 3.1(a-e) it can be seen that the general trends are;

Lucilia cuprina.

A generally contagious distribution, with some indication of random distribution at lower densities.

Lucilia sericata.

Consistently contagious distributions at all sites and densities.

Calliphora stygia.

A highly contagious distribution in comparison to the other species.

Calliphora hilli.

Distribution is more or less random, where contagious distributions are indicated this is due to low incidence of this species in the traps.

Calliphora vicina.

A generally random distribution.

Chrysomya rufifacies.

Contagious distribution is more indicative of the low densities at which this species was trapped.

Date	<i>L.c</i>	<i>L.s</i>	Species	<i>C.h</i>	<i>C.v</i>	<i>Ch.r</i>
			<i>C.s</i>			
821108	-	-	-	-	-	-
821120	-0.23	1.08	2.63	0.03	0.45	-
821206	4.40	8.04	10.13	0.21	-	-
821219	-0.32	0.02	-0.10	42.60	42.60	-
830119	0.65	2.45	24.31	1.83	-	-
830131	2.68	47.45	2.73	0.10	-	-
830302	2.94	2.80	7.81	-0.04	-	-

Table 3.1a : Values of I_{DM} for Site 1 (Pontville).

Date	<i>L.c</i>	<i>L.s</i>	Species	<i>C.h</i>	<i>C.v</i>	<i>Ch.r</i>
			<i>C.s</i>			
821109	-	-	-	-	-	-
821121	2.52	0.23	12.22	1.56	-	-
821207	-	-	42.65	0.87	-	-
821220	0.98	-	9.53	0.10	-	-
830120	0.11	0.02	2.37	-0.01	-	-
830201	3.21	0.80	7.02	1.29	-	-

Table 3.1b : Values of I_{DM} for Site 2 (Bothwell).

Date	<i>L.c</i>	<i>L.s</i>	Species	<i>C.h</i>	<i>C.v</i>	<i>Ch.r</i>
			<i>C.s</i>			
821110	-	-	-	-	-	-
821122	1.25	0.02	13.05	0.37	-	-
821221	8.94	5.07	23.90	0.37	73.4	-
830121	3.85	0.01	1.50	11.13	-	-
830202	3.83	23.47	17.71	0.90	-	-
830303	18.81	2.59	0.92	0.77	17.90	17.90

Table 3.1c : Values of I_{DM} for Site 3 (Ross).

Date	<i>L.c</i>	<i>L.s</i>	Species <i>C.s</i>	<i>C.h</i>	<i>C.v</i>	<i>Ch.r</i>
821111	-	-	-	-	-	-
821123	5.04	1.60	50.05	6.01	2.46	-
821222	8.91	-0.12	4.67	1.32	17.90	-
830122	22.10	24.02	55.48	21.00	-	-
830203	21.49	9.76	22.95	0.73	-	17.90
830304	18.57	22.16	9.46	0.84	0.02	-0.20

Table 3.1d : Values of I_{DM} for Site 4 (Powranna).

Date	<i>L.c</i>	<i>L.s</i>	Species <i>C.s</i>	<i>C.h</i>	<i>C.v</i>	<i>Ch.r</i>
821124	-0.23	-	8.79	1.23	0.81	-
821223	7.92	-	24.69	3.25	-	17.90
830204	158.71	17.90	32.66	0.56	-	8.32

Table 3.1e : Values of I_{DM} for Site 5 (Springfield).

b. Regular lattice trap design.

Contour graphs of fly density against grid layout generated by SURFACE 2 for raw data collected with the regular lattice sampling strategy are presented in Figure 3.7 (a-e). They are not discussed here but may be used as a guide to the correlograms presented in Figure 3.8 (a-e). The correlograms show the index of spatial interaction of fly density against grid distance between traps. I_{Mc} may be interpreted as follows.

$I_{Mc} > 0$ clumping of individuals over short grid distances (low order) or clumping of groups over longer grid distances (high order),

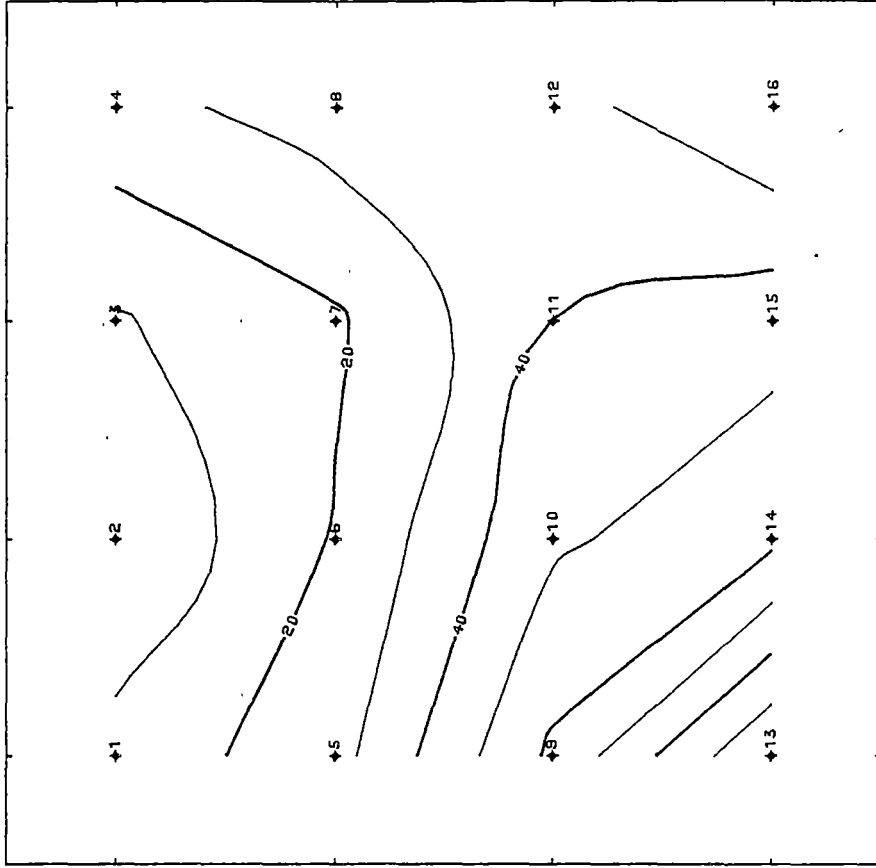
$I_{Mc} = 0$ no interaction,

$I_{Mc} < 0$ repulsion of individuals over short grid distances (low order) or repulsion of groups over longer grid distances (high order).

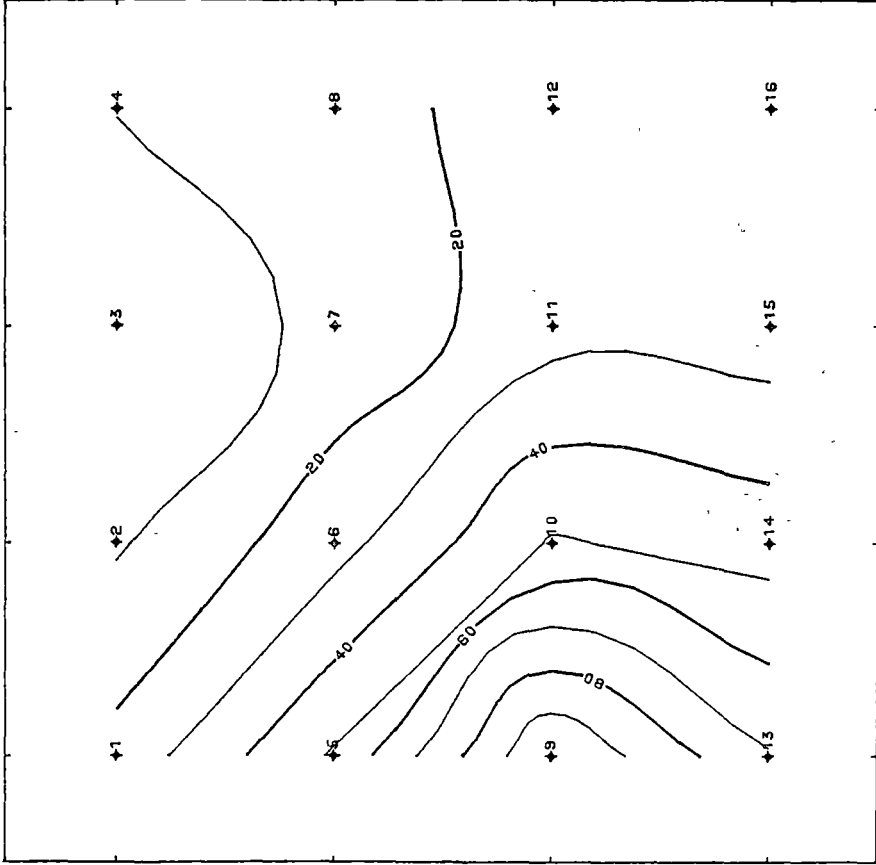
Figure 3.7a. Distribution of *L. cuprina* over the trapping grid by trapping day (YYMMDD). The location of traps is indicated by + .



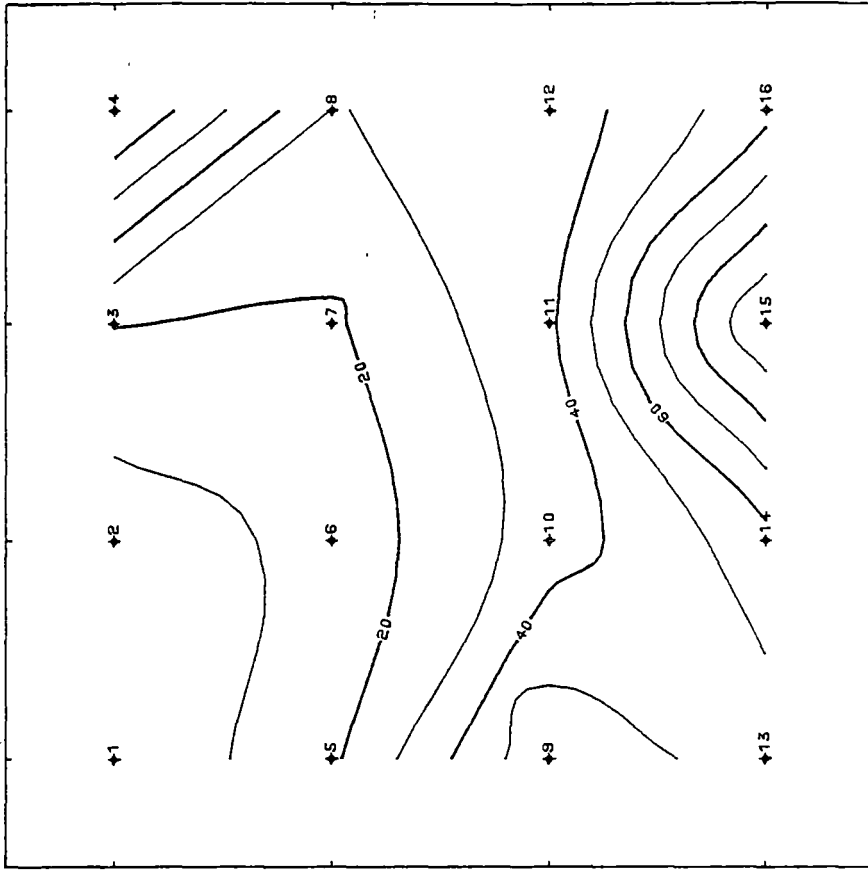
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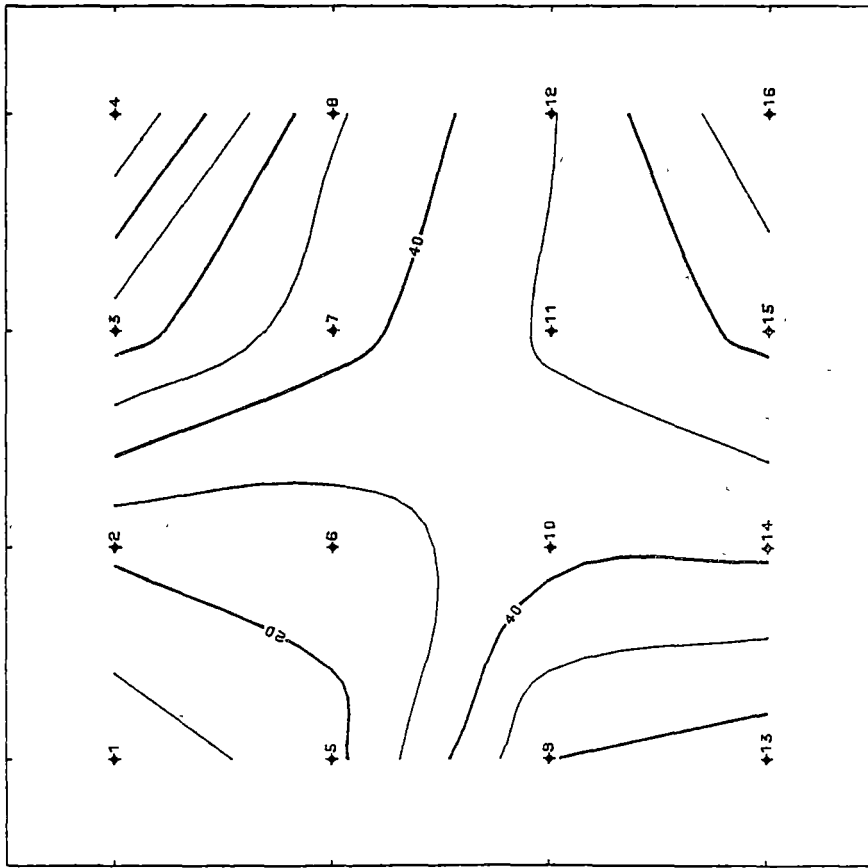
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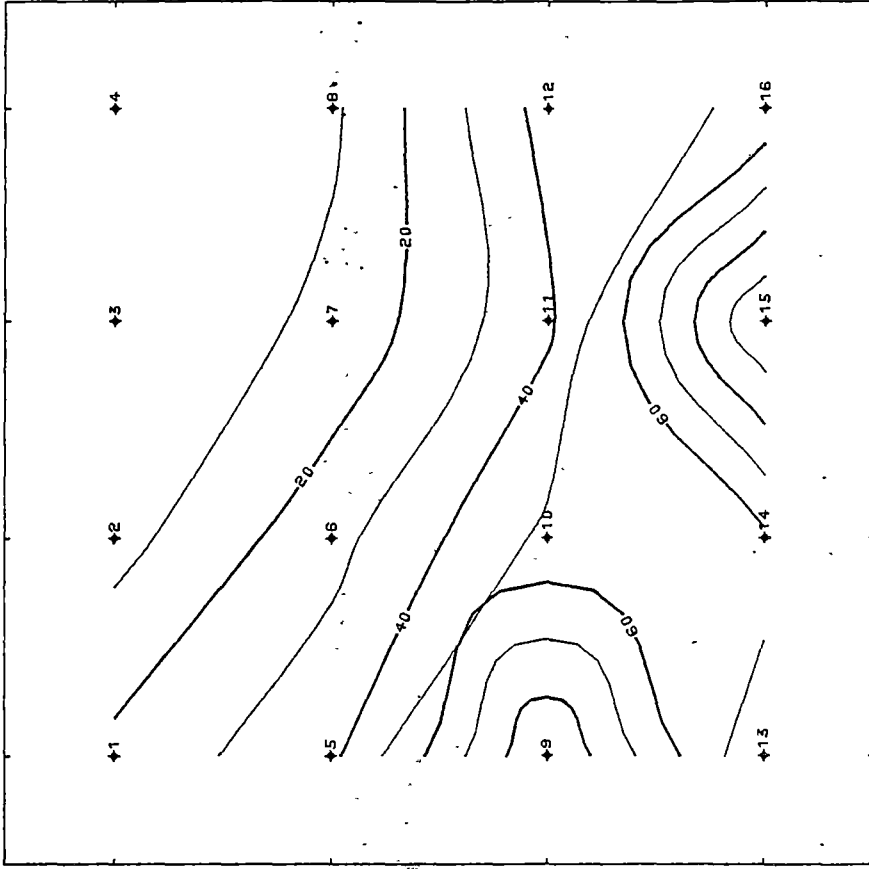
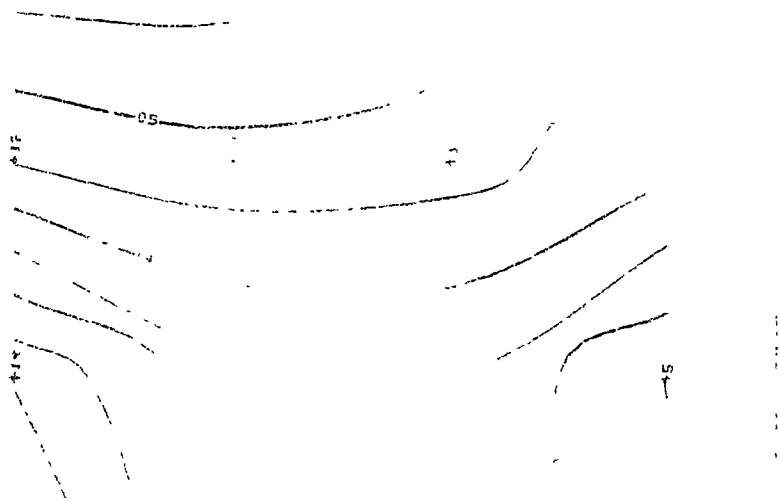
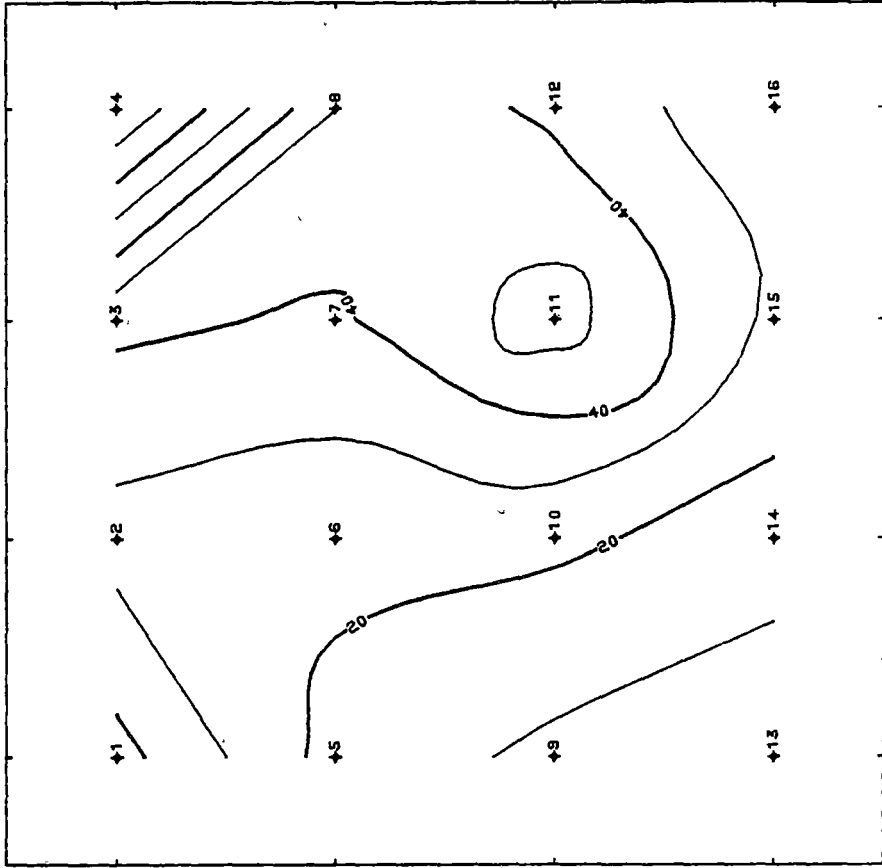


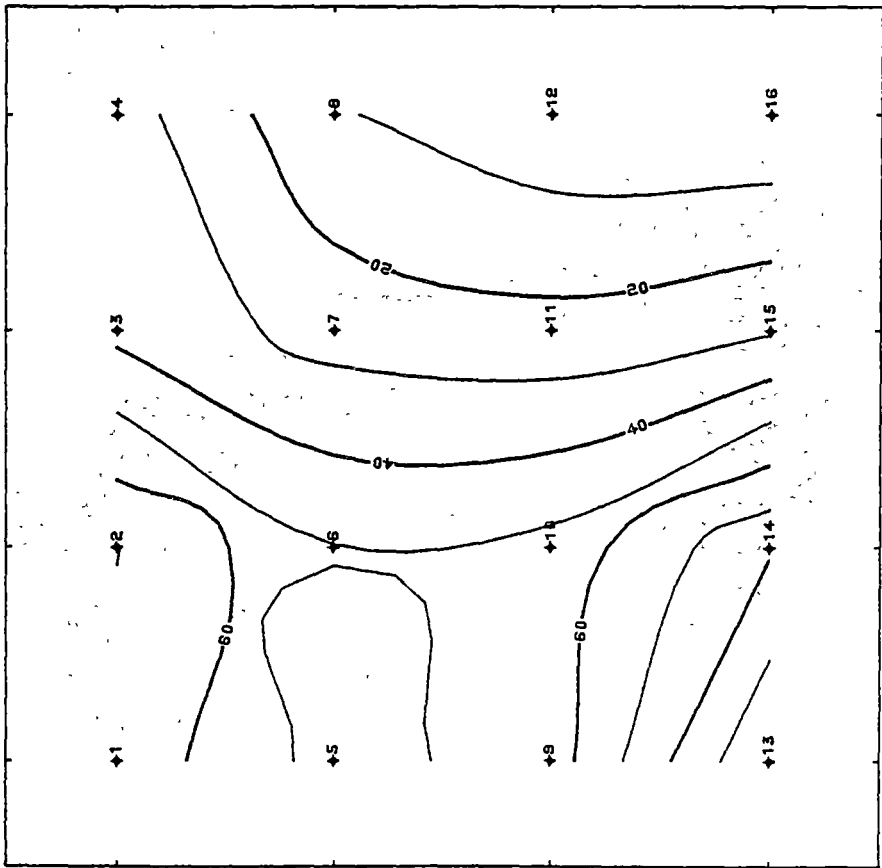
Figure 3.7b. Distribution of *L. sericata* over the trapping grid by trapping day (YYMMDD). The location of traps is indicated by + .



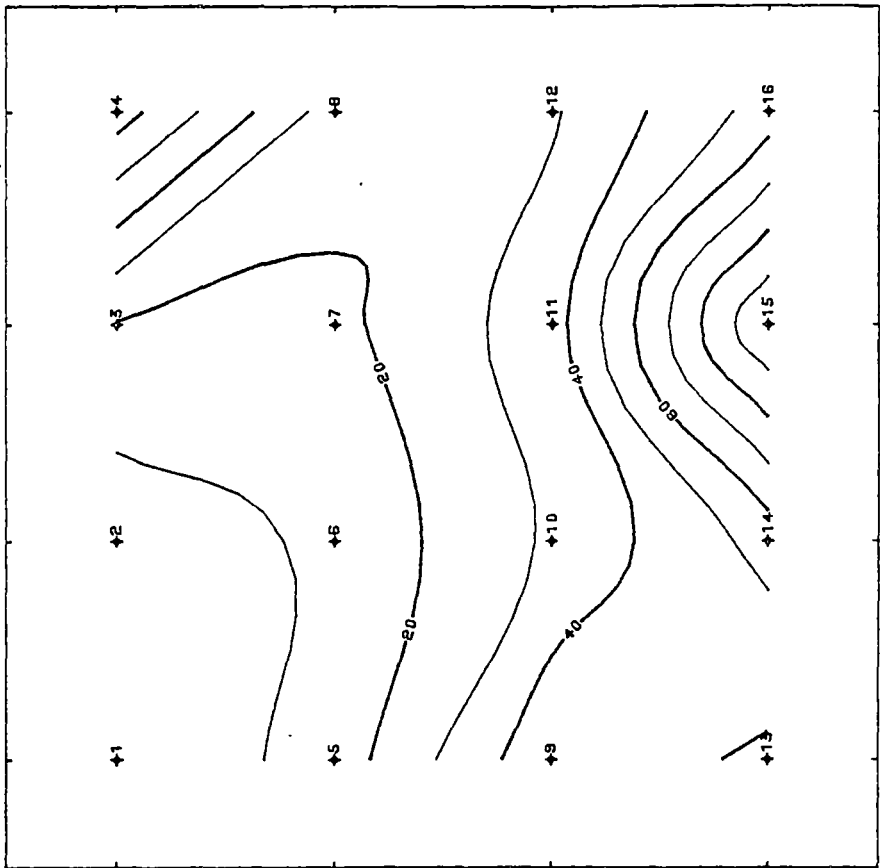
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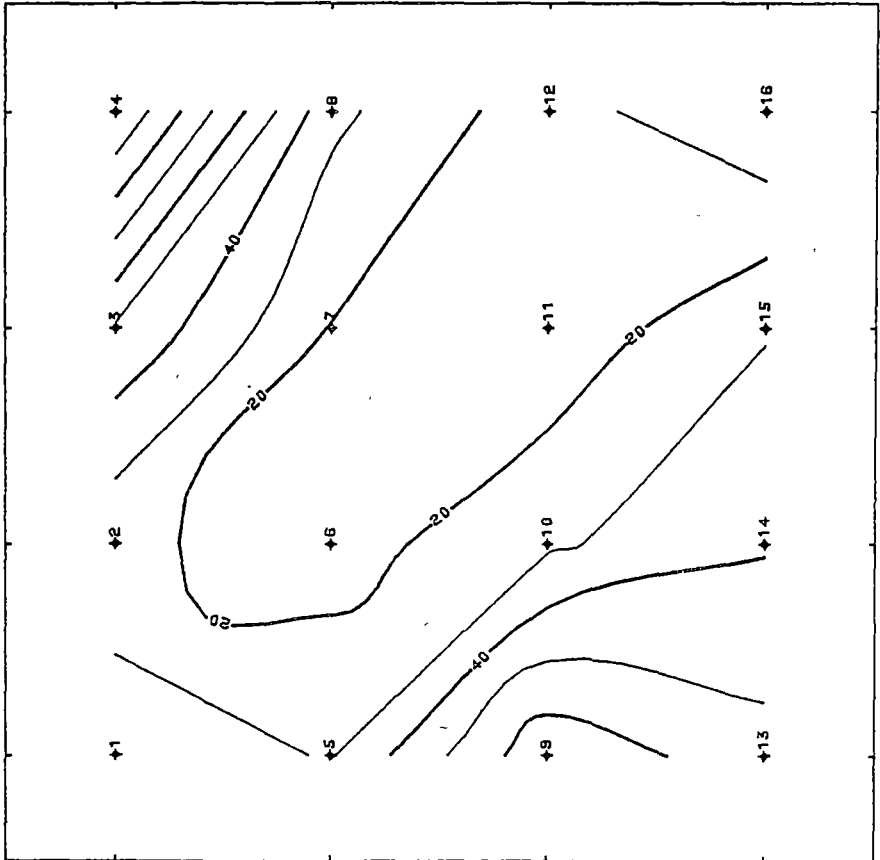
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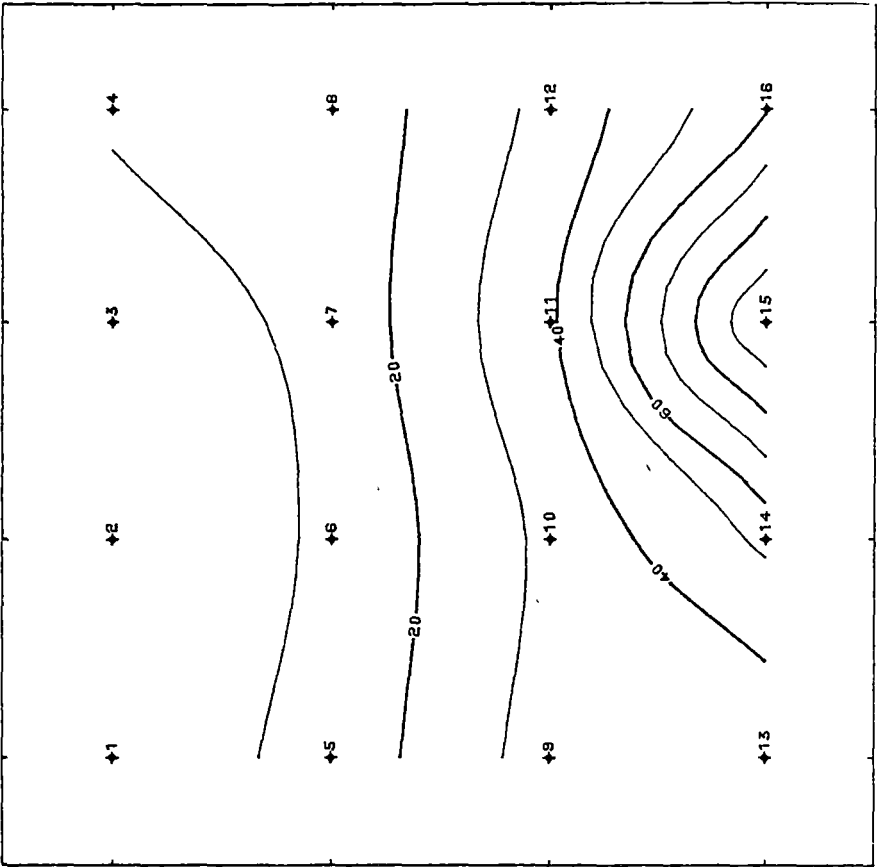
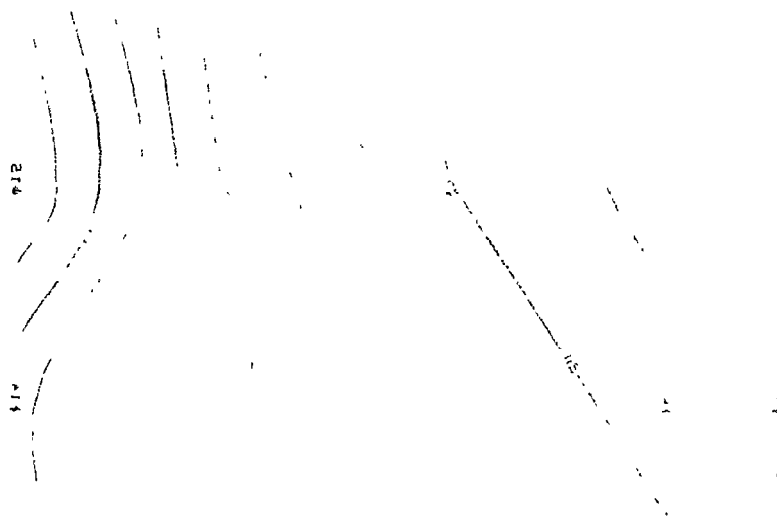
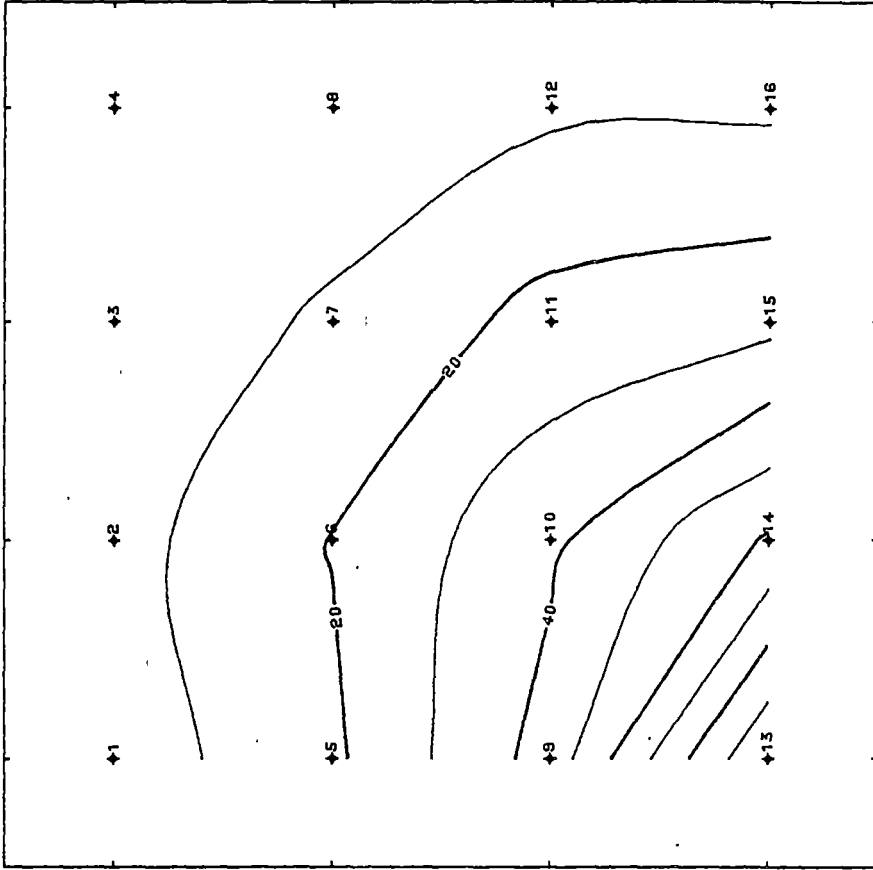


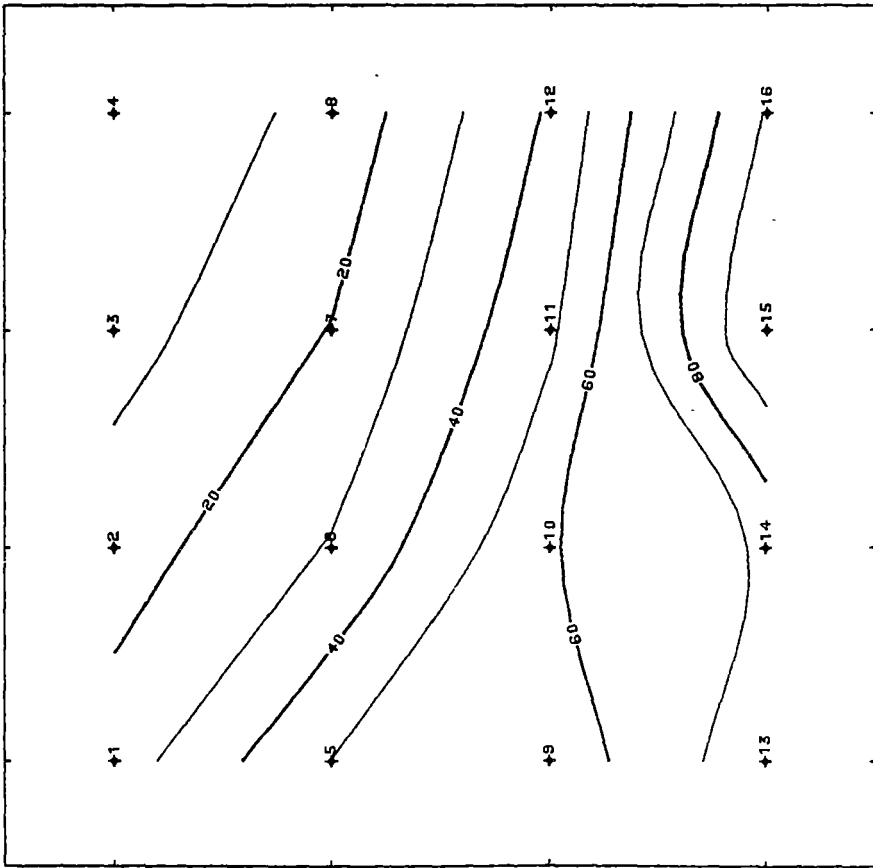
Figure 3.7c. Distribution of *C. stygia* over the trapping grid by trapping day (YYMMDD). The location of traps is indicated by + .



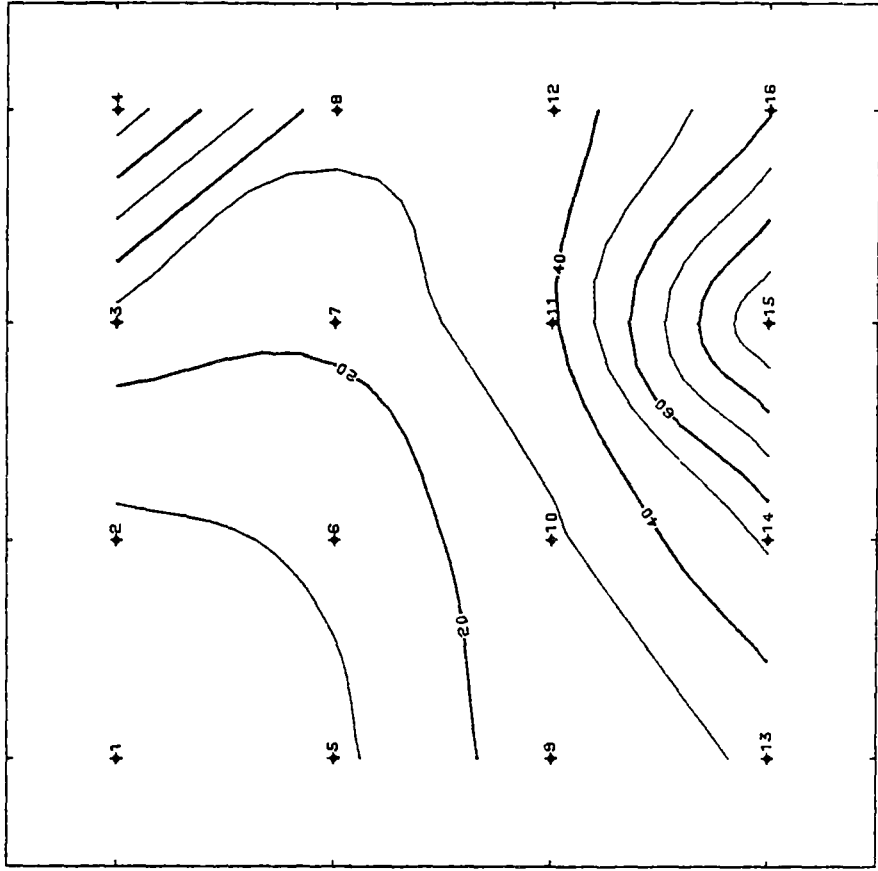
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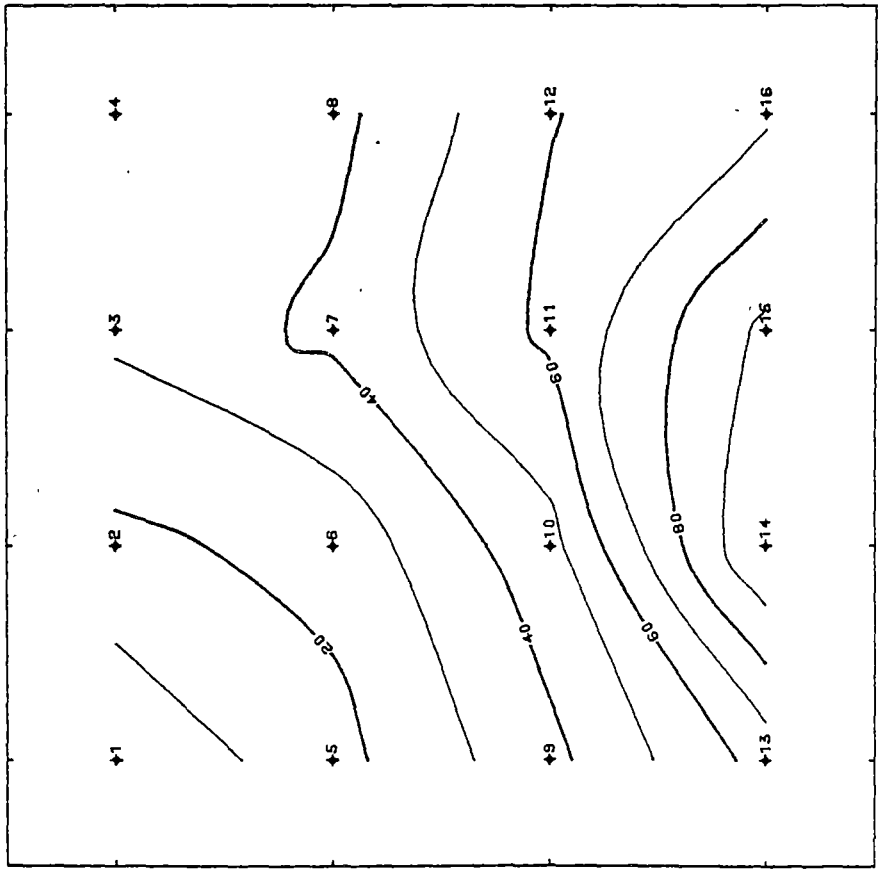
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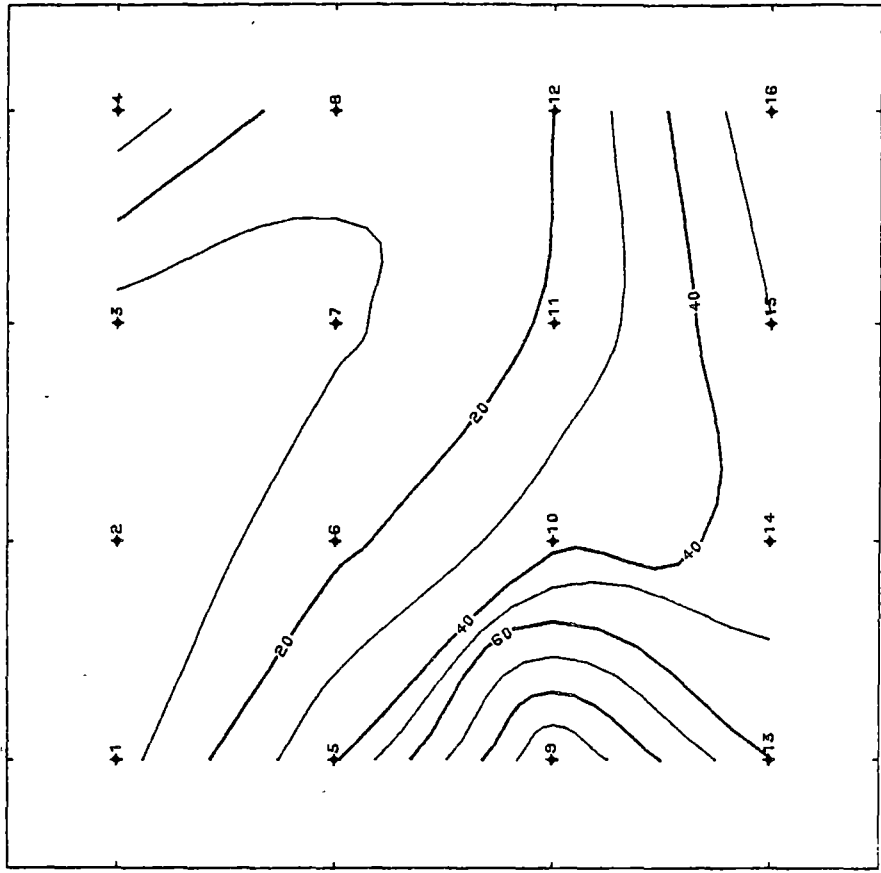
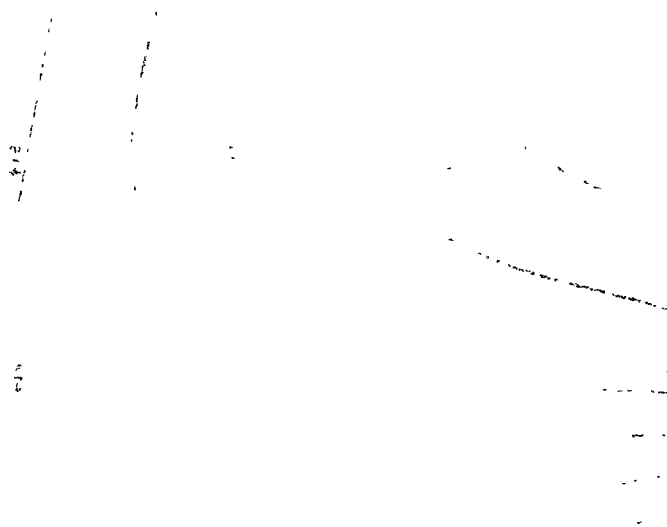
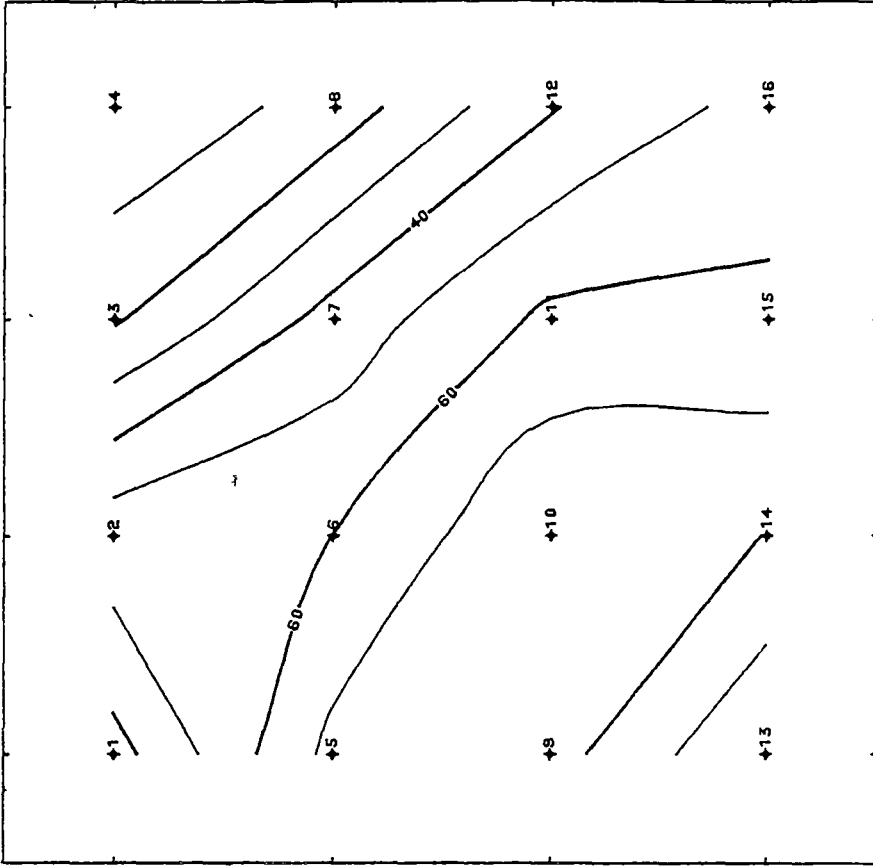


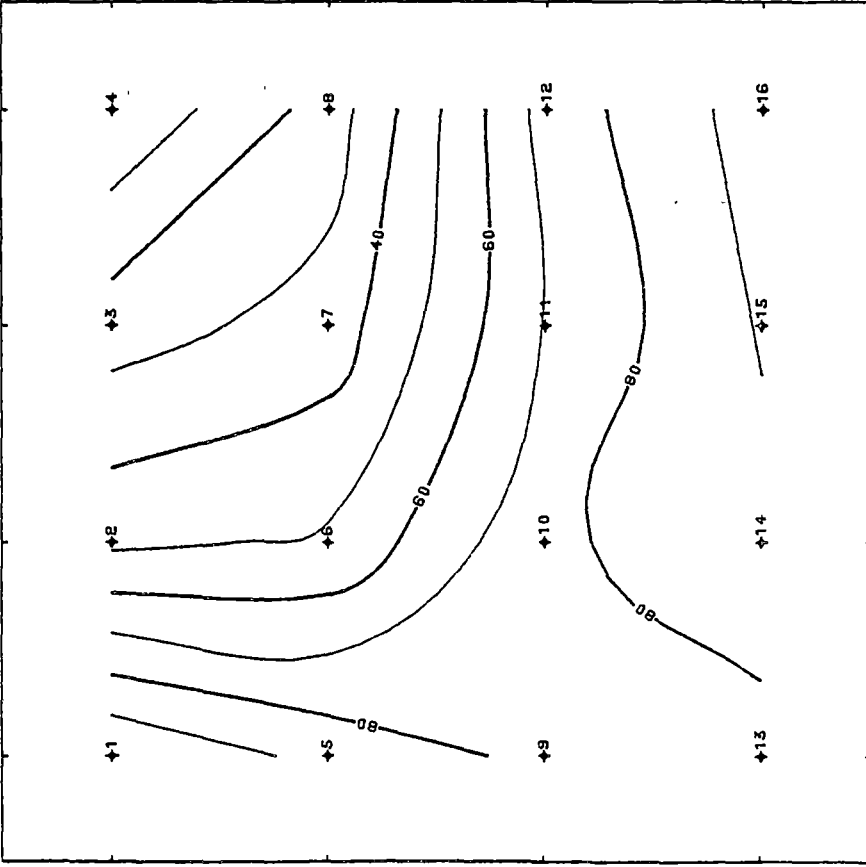
Figure 3.7d. Distribution of *C. hilli* over the trapping grid by trapping day (YYMMDD). The location of traps is indicated by + .



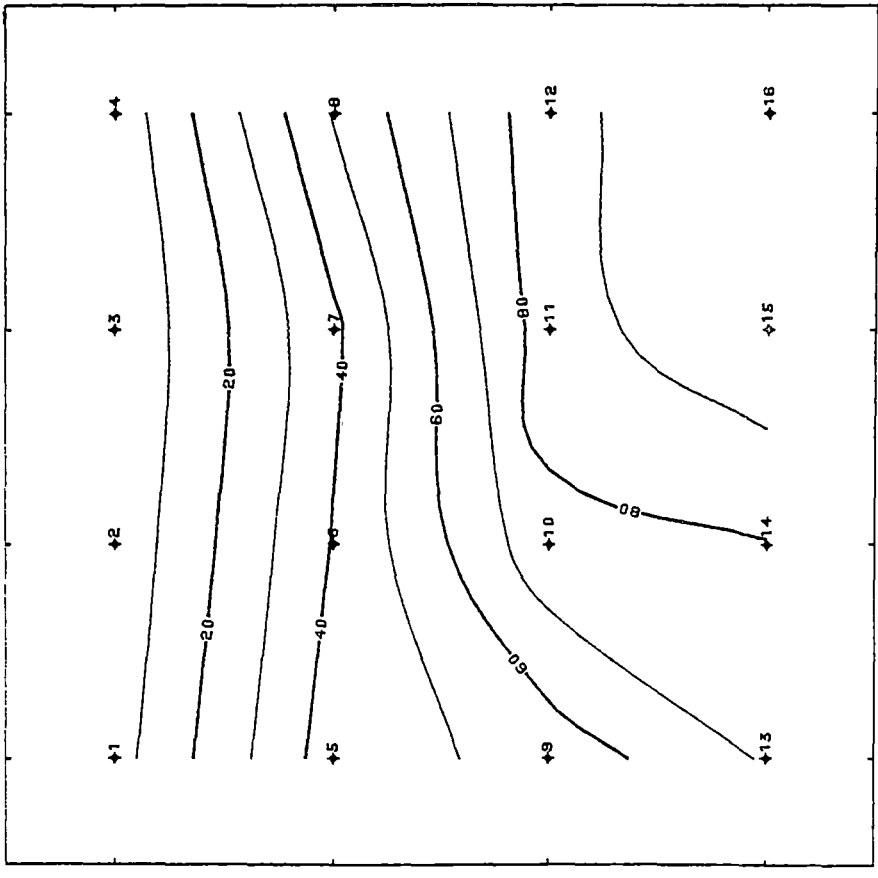
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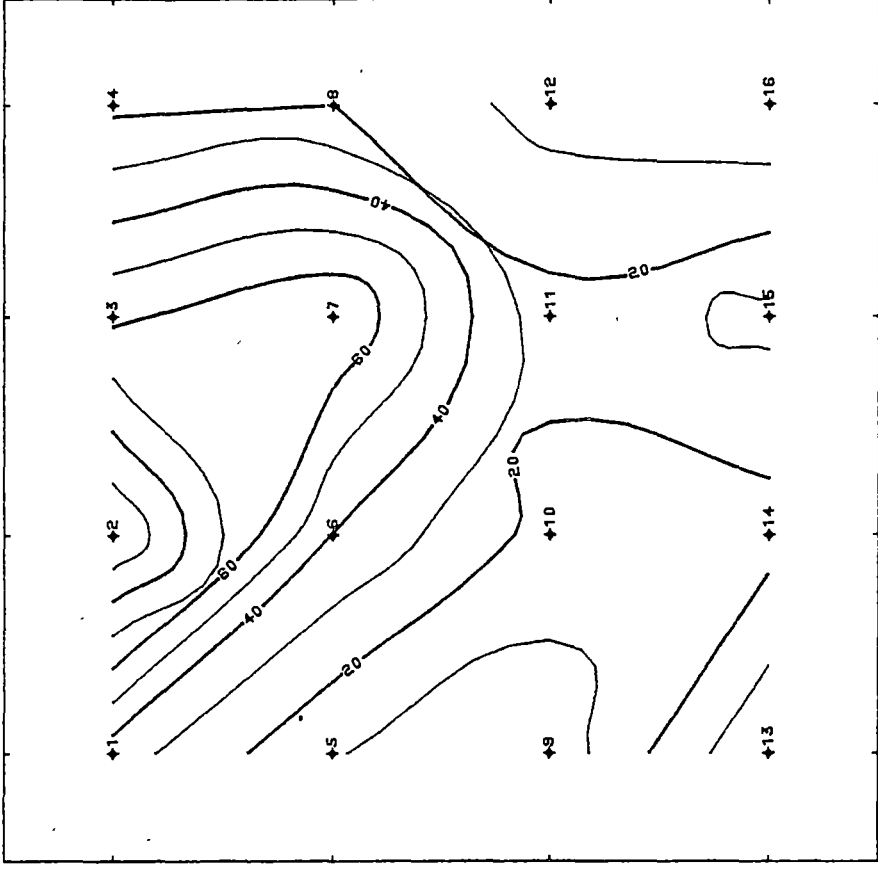
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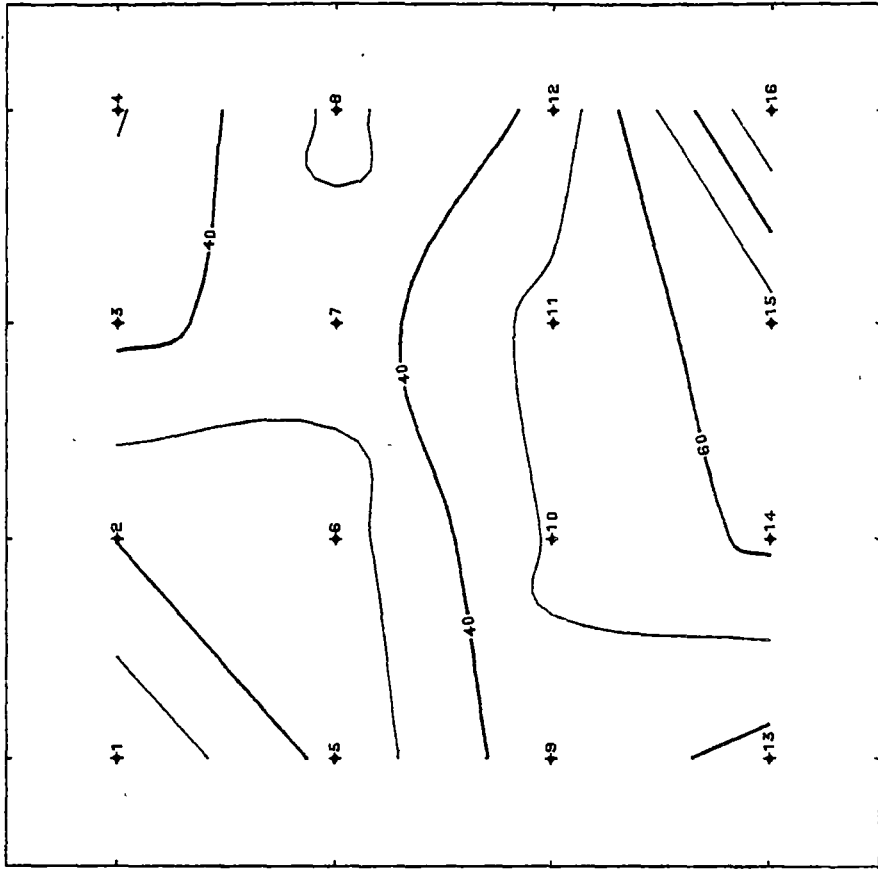
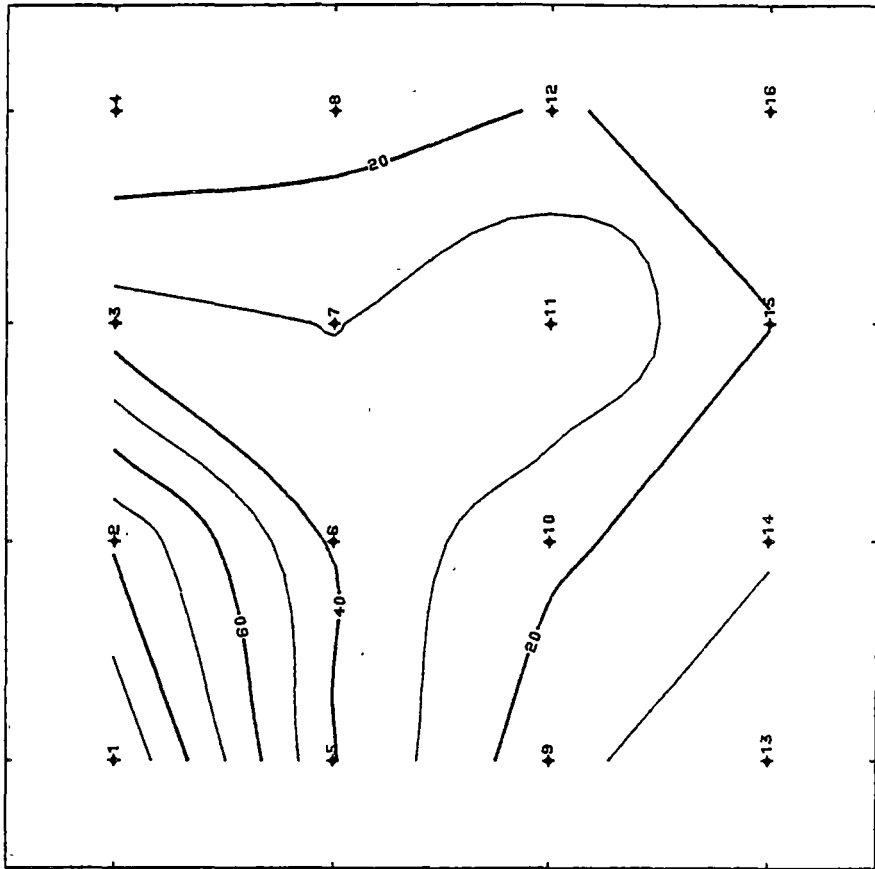


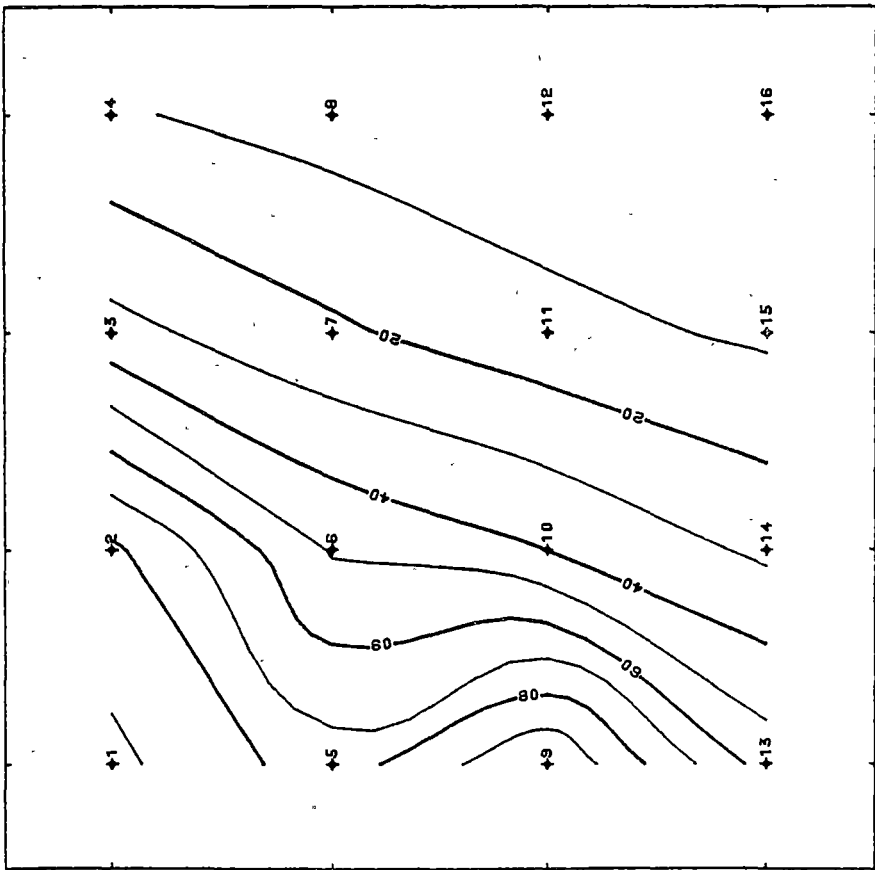
Figure 3.7e. Distribution of *Ch. rufifacies* over the trapping grid by trapping day (YYMMDD).
The location of traps is indicated by + .



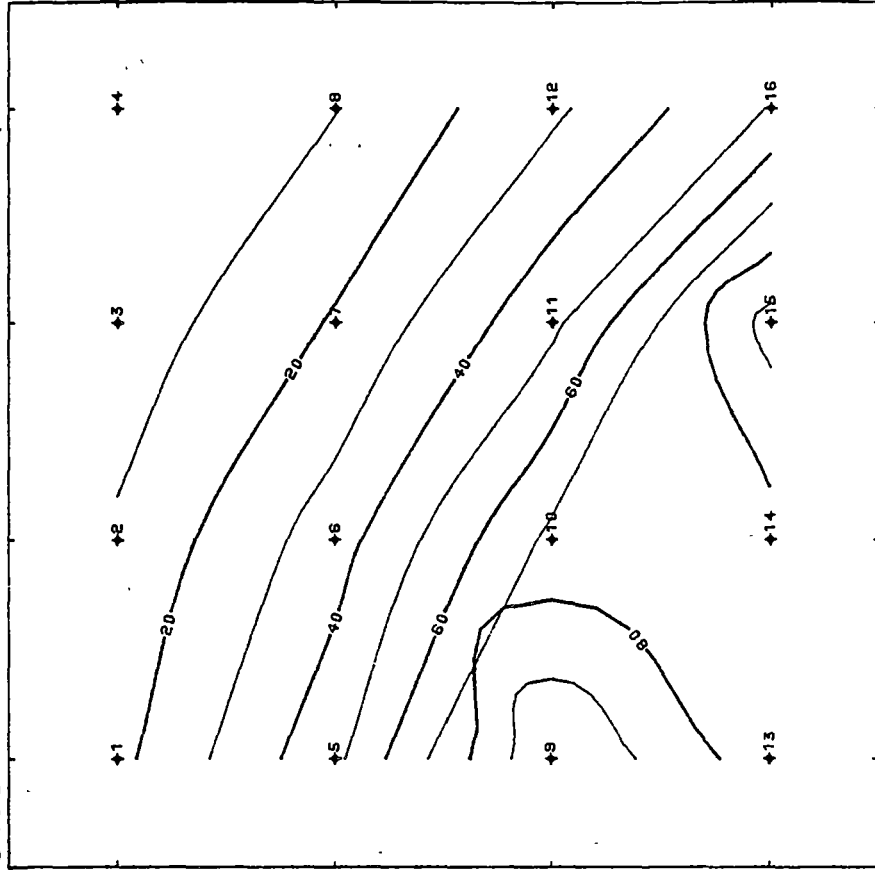
840305



840226



840317



840311

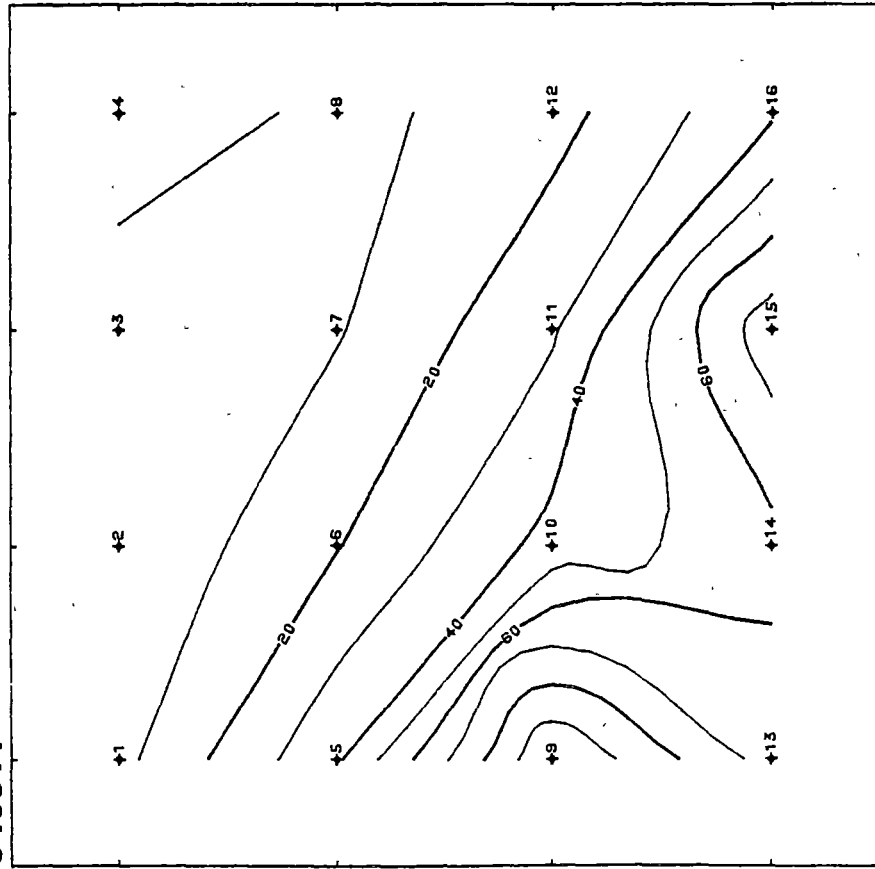
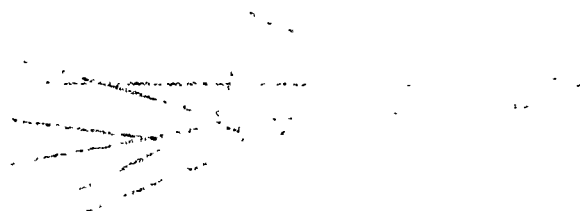
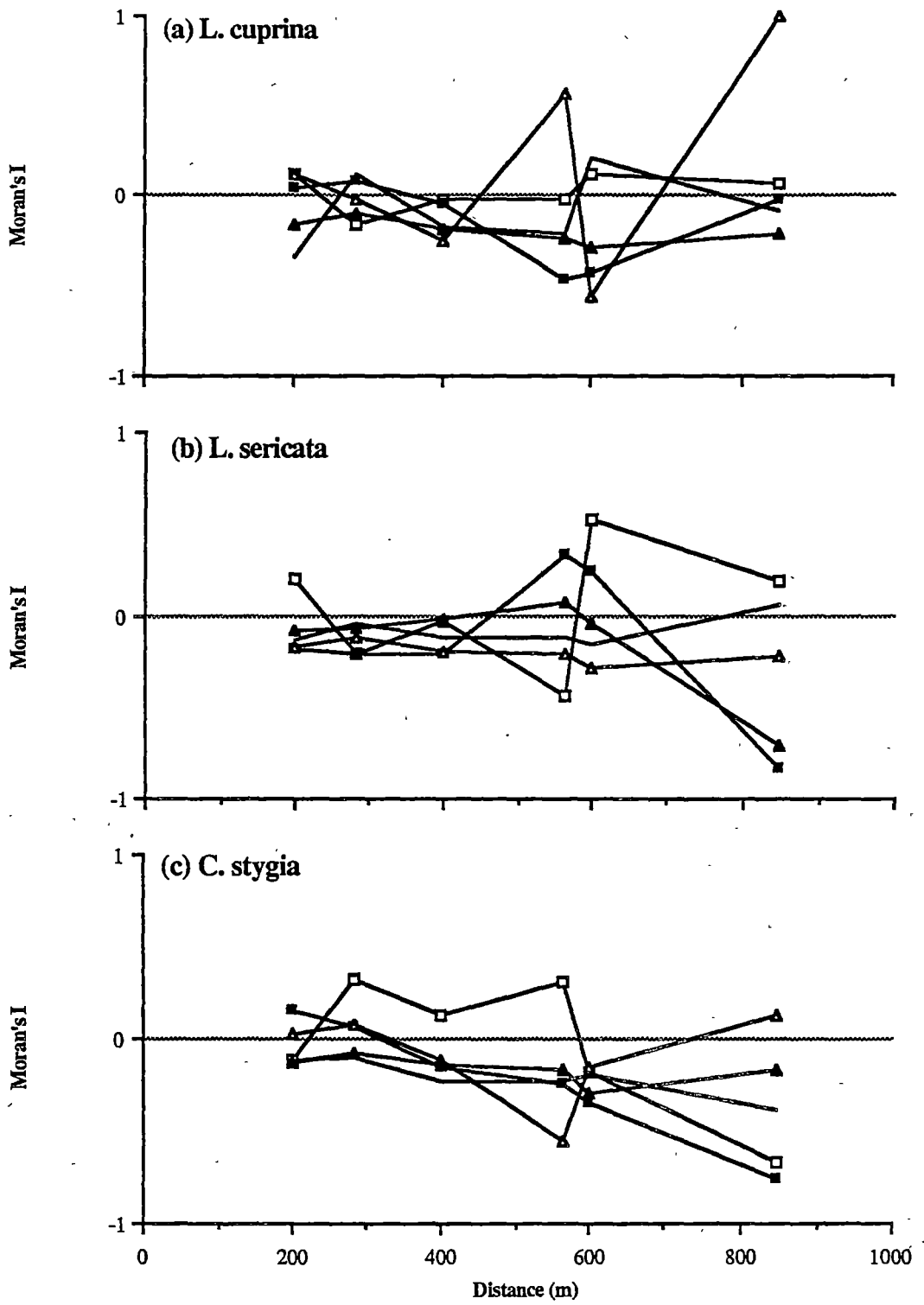
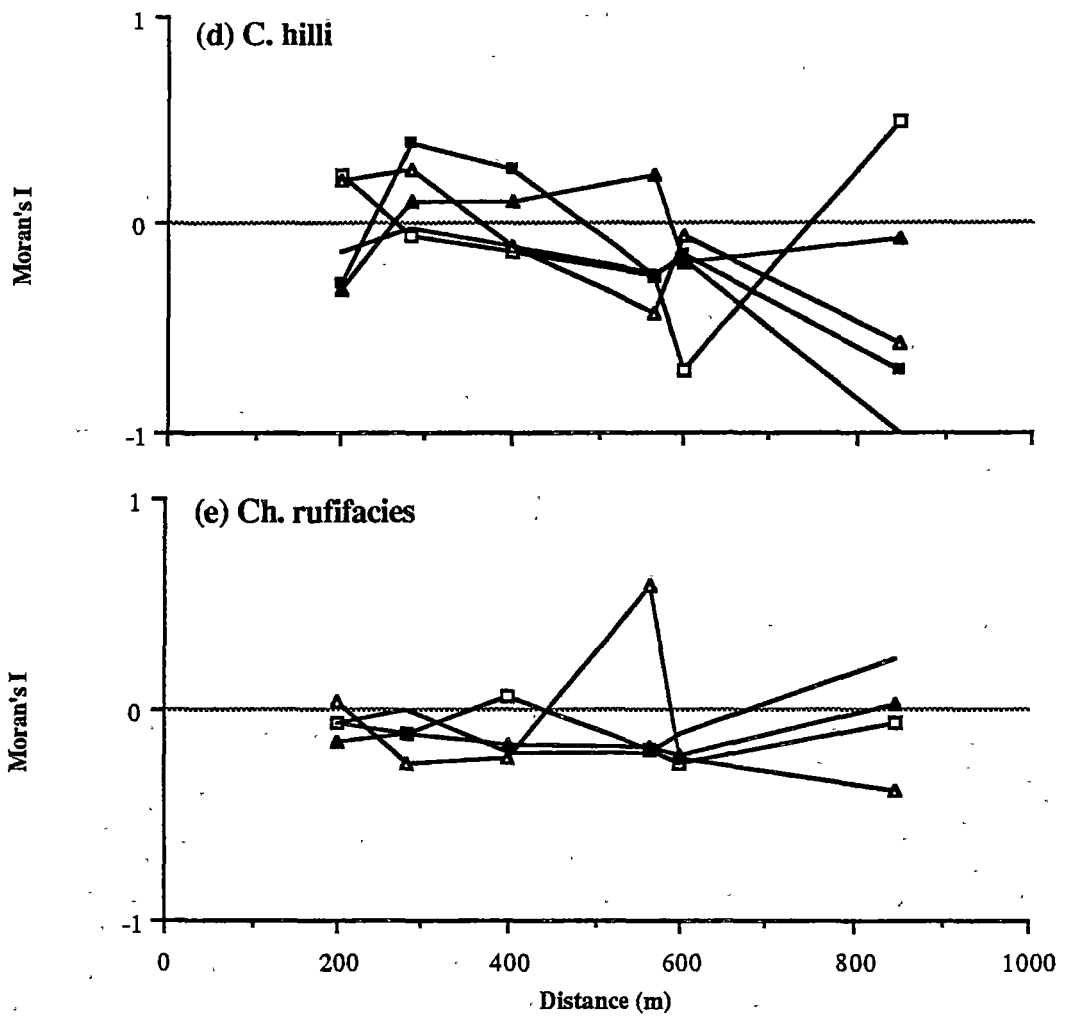


Figure 3.8. Correlograms of the autocorrelation of fly abundance against distance, for each species and trapping day. Trapping dates are given in the form YYMMDD.







As will be described later (Chapter 5) interaction may often be strong within cohorts or age classes of flies. Because of this, interactions in the following grouped data may be confounded. It is therefore not valid to examine the results in any detail. Instead the trends in the correlograms for the species are useful. These trends are;

Lucilia cuprina .

Interaction is weak or absent over short distances. The index I_{Mc} becomes more variable with distance but the average value is still weakly negative. The overall trend is a constant level of weak negative interaction, indicating a clumpy distribution. Patches (or clumps) are likely to be smaller in diameter than the grid dimensions. This is further indicated by the strong positive high order autocorrelation seen at 800m and at 483m (Fig. 3.8a) which indicate that strong nodes exist within these distances.

Lucilia sericata .

Again interaction is weak or absent over short distances. However the intensity of the negative autocorrelation increases with distance. Whilst the overall trend is similar to that of *L. cuprina* the indication of clumping is stronger. Patches of *L. sericata* appear to be smaller than those of *L. cuprina* , the adults probably being more sedentary.

Calliphora stygia .

The trend here is stronger than for the *Lucilia* spp. There is no strong positive or negative autocorrelation at short distances. With increased grid distance, autocorrelation becomes negative. This pattern suggests that the flies distribution is patchy but that the patch size is greater than the total grid size. This would result in a homogenous distribution of flies within the trapping grid, that is the clump is centered over the grid.

Calliphora hilli .

As with *C. stygia* the trend in this correlogram is strong. At the smallest distance (200m) autocorrelation is scattered around 0. With increased distance autocorrelation becomes generally positive (at around 200-400). From this point it decreases and becomes strongly negative at the maximum distance. This suggests that this species also has a patchy distribution but that while patches are large resulting in a basically homogenous distribution some sites are biased in attractiveness resulting in a secondary small scale pattern of clumping or that the clump is not centered over the grid but that two or more clumps overlap on the grid.

Chrysomya rufifacies .

The weak autocorrelation seen here remains more or less constant for all the distances considered. As with *L. cuprina* this suggests that the distribution is highly clumped. In this case this is more likely to be an artifact of the small number of individuals actually sampled. At such low levels of abundance many trap sites will record no catch of *Ch. rufifacies* , so rather than measuring interaction the correlogram is showing the rarity of this species occurrence.

3.2.2.2 Inter-specific effects

Results of the analysis of inter-specific autocorrelation for each trapping session (day) are presented in Table 3.2(a-e). Autocorrelations are calculated for grid distances of 0 (ie. components at the same trap site) and 1 (ie. components from the nearest neighbour to the trap site). As with the section above dealing with intra-specific autocorrelation the values of I_{Mc} are interpreted in the same way, although only low order distances are considered in the analysis. Trends from Table 3.2 by species are as follows.

Lucilia cuprina .

A strong positive correlation of *L. cuprina* to live sheep at a grid distance of 0 is seen. Positive correlations of *L. cuprina* are also seen with *Ch. rufifacies* and *L. sericata* but are probably due more to the concomitant attraction of these species to live sheep too. Strong attraction to sheep is only seen on the trapping days prior to the placement of the experimental carcasses. When the carcasses are present *L. cuprina* is highly correlated with both the carcasses and the other flies attracted to the carcasses.

Lucilia sericata .

The positive correlation of *L. sericata* to live sheep is not as strong or consistent as with *L. cuprina* . However the attraction to fresh carcasses are as strong as that of *L. cuprina* . A positive correlation is seen with *C. hilli* at a grid distance of 1 at the last trap session. This may be a by-product of the differential attractiveness of the carcasses. That is, the carcasses represent strong nodes of *L. sericata* distribution, but if *C. hilli* is not attracted then an appearance of distance linked correlation is given. This is borne out by the absence of a significant autocorrelation between *C. hilli* and the carcasses.

Calliphora stygia .

This species shows no particularly strong autocorrelations with other flies. There is however a significant positive correlation with the carcasses. This attraction appears to be stronger to the older carcasses.

Calliphora hilli .

No significant autocorrelations are seen with the other species or the distribution of live sheep. This is the only species without a significant autocorrelation with the carcasses on the last trap day.

Chrysomya rufifacies .

This species shows an occasional significant positive correlation with live sheep. A strong positive correlation with carcasses is seen.

General relationships.

Where strong positive correlations occur between species of flies and live sheep at a distance of 0, they are often accompanied by a negative correlation between the species pairs at a distance of 1. This suggests localised depletion of sites around the source of attraction and thus an appearance of repulsion. This is seen with all the species for the fresh carcass, and all except *C. hilli* with the older carcass (ie the value of I_{Mc} is consistently negative for comparison pairs involving the carcass at a distance of 1).

Date: 840226	Grid distance = 0						
SPECIES	<i>Lc</i>	<i>Ls</i>	<i>Cs</i>	<i>Ch</i>	<i>Chr</i>	<i>S1.</i>	<i>S2.</i>
L.c	-	1.00	-0.16	0.12	-0.11**	-0.11***	-
L.s		-	-0.16	0.12	-0.11	-0.11	-
C.s			-	0.36	-0.27	0.00	-
C.h				-	-0.02	0.11	-
Chr					-	0.49*	-
S1						-	-
Grid distance = 1							
L.c	-	-0.07	0.42	0.13	-0.11	0.11	-
L.s		-	0.42	0.13	-0.16	0.11	-
C.s			-	0.17	0.16	0.03	-
C.h				-	0.18	0.02	-
Chr					-	0.04	-
S1						-	-

Table 3.2 (a). Inter-specific autocorrelation for 26/2/84.

Date: 840303	Grid distance = 0						
SPECIES	<i>Lc</i>	<i>Ls</i>	<i>Cs</i>	<i>Ch</i>	<i>Chr</i>	<i>S1.</i>	<i>S2.</i>
L.c	-	0.00	0.71***	0.25	0.00	0.57**	-
L.s		-	-0.13	-0.21	0.00	0.14	-
C.s			-	0.47*	0.00	0.30	-
C.h				-	0.00	-0.05	-
Chr					-	0.00	-
S1						-	-
Grid distance = 1							
L.c	-	0.00	-0.08*	-0.26	0.00	0.04	-
L.s		-	-0.07	-0.26	0.00	0.04	-
C.s			-	0.12	0.00	0.22	-
C.h				-	0.00	0.16	-
Chr					-	0.00	-
S1						-	-

Table 3.2 (b). Inter-specific autocorrelation for 3/3/84.

Date: 840305		Grid distance = 0					
SPECIES	<i>Lc</i>	<i>Ls</i>	<i>Cs</i>	<i>Ch</i>	<i>Chr</i>	<i>S1.</i>	<i>S2.</i>
L.c	-	0.56**	0.35	-0.14	-0.32	0.29**	-
L.s		-	-0.04	-0.28	0.07	0.20*	-
C.s			-	0.03	-0.14	-0.12	-
C.h				-	-0.14	-0.32	-
Ch.r					-	-0.31	-
S1						-	-
		Grid distance = 1					
L.c	-	-0.03*	0.09	-0.13	0.15	-0.02	-
L.s		-	0.14*	-0.24	0.19	-0.06	-
C.s			-	0.36**	-0.09	-0.06	-
C.h				-	-0.07	-0.02	-
Ch.r					-	-0.05	-
S1						-	-

Table 3.2 (c). Inter-specific autocorrelation for 5/3/84.

Date: 840311		Grid distance = 0					
SPECIES	<i>Lc</i>	<i>Ls</i>	<i>Cs</i>	<i>Ch</i>	<i>Chr</i>	<i>S1.</i>	<i>S2.</i>
L.c	-	0.86***	0.85***	0.05	0.96***	-0.04	0.99***
L.s		-	0.87***	0.14	0.86***	-0.09	0.93***
C.s			-	0.12	0.66**	-0.05	0.75***
C.h				-	0.01	-0.09	0.04
Ch.r					-	-0.03	0.99***
S1						-	-0.04
		Grid distance = 1					
L.c	-	-0.17	-0.11	-0.11	-0.17	0.06	-0.17
L.s		-	-0.14	-0.10	-0.18	-0.02	-0.18
C.s			-	-0.19	-0.14	-0.08	-0.14
C.h				-	-0.13	-0.16	-0.14
Ch.r					-	0.09	-0.17
S1						-	0.06

Table 3.2 (d). Inter-specific autocorrelation for 11/3/84.

Date: 840317	Grid distance = 0						
SPECIES	<i>L.c</i>	<i>L.s</i>	<i>C.s</i>	<i>Ch</i>	<i>Ch.r</i>	<i>S1.</i>	<i>S2.</i>
<i>L.c</i>	-	0.51**	0.45*	-0.03	0.40	0.14	0.55**
<i>L.s</i>		-	0.07	-0.07	0.62**	0.15	0.49*
<i>C.s</i>			-	0.41*	0.72***	0.34	0.83***
<i>C.h</i>				-	0.12	0.21	0.09
<i>Ch.r</i>					-	0.52*	0.92***
<i>S1</i>						-	0.24
Grid distance = 1							
<i>L.c</i>	-	-0.10	-0.03	0.19*	-0.04	-0.13	-0.03*
<i>L.s</i>		-	0.04	0.33**	-0.16	0.14	-0.13
<i>C.s</i>			-	0.01	-0.02	0.00	-0.09
<i>C.h</i>				-	0.25*	0.01	0.21
<i>Ch.r</i>					-	0.1	-0.11
<i>S1</i>						-	0.00

Table 3.2 (e). Inter-specific autocorrelation for 17/3/84.

L.c = *L. cuprina*, *L.s* = *L. sericata*, *C.s* = *C. stygia*, *C.h* = *C. hilli*, *Ch.r* = *Ch. rufifacies*, *S1* = flock size/proximity index, *S2* = experimental carcasses.

$P > 0.1$; * = significant, $0.1 \geq P > 0.05$; ** = highly significant, $0.05 \geq P > 0.01$; *** = very highly significant, $P \leq 0.01$.

3.2.3 CARRION EXPERIMENTS

3.2.3.1 Competition in the presence of *Chrysomya*

Emergence records from this experiment are given in Table 3.3(a-c). Included in these tables are the catches from traps set adjacent to the carcasses for the period before first emergences were recorded. Carcass 1 was placed at trap cell 9 (the site for mean highest *L. cuprina* abundance), Carcass 2 at trap cell 4 (the site for mean highest *L. sericata* abundance) and Carcass 3 at trap cell 15 (the site for mean highest *L. cuprina* and *L. sericata* combined abundance).

Date	<i>L.c</i>	<i>L.s</i>	Species <i>C.s</i>	<i>C.h</i>	<i>Ch.r</i>	<i>Ch.v</i>
Trap data						
840311	112	60	5	-	94	-
840317	32	13	3	3	2	-
Emergence data						
840323	-	-	-	-	87	-
840329	-	-	-	-	1652	-
840405	-	-	-	-	3501	-
840412	-	-	25	-	1051	-
Total emerging	-	-	25	-	6291	-

Table 3.3a. Emergence and trap records by date and species for Carcass 1.

Date	<i>L.c</i>	<i>L.s</i>	Species <i>C.s</i>	<i>C.h</i>	<i>Ch.r</i>	<i>Ch.v</i>
Trap data						
840311	112	68	16	-	20	-
840317	13	5	1	3	-	-
Emergence data						
840323	-	-	-	-	-	-
840329	-	-	-	-	113	10
840405	-	-	-	-	1069	-
840412	-	11	12	-	978	-
Total emerging	-	11	12	-	2160	10

Table 3.3b. Emergence and trap records by date and species for Carcass 2.

Date	<i>L.c</i>	<i>L.s</i>	Species <i>C.s</i>	<i>C.h</i>	<i>Ch.r</i>	<i>Ch.v</i>
Trap data						
840311	191	131	27	1	70	-
840317	34	45	1	1	2	-
Emergence data						
840323	-	8	-	-	136	-
840329	-	-	-	-	1178	-
840405	-	-	-	-	1339	-
840412	-	-	4	-	700	-
Total emerging	-	8	4	-	3353	-

Table 3.3c. Emergence and trap records by date and species for Carcass 3.

Generally the abundance of species trapped bears no relation to the subsequent emergences. That the traps give some measure of the attractiveness of the carcass rather than their own inherent attractiveness can be seen by comparing the catches of traps next to carcasses (as given in Table 3.3) to the mean catch of traps set on the same days at the other trap cells (without close proximity to carcasses). These figures are contrasted in Table 3.4.

Date	<i>L.c</i>	<i>L.s</i>	Species <i>C.s</i>	<i>C.h</i>	<i>Ch.r</i>	<i>Ch.v</i>
With carcasss						
840311	138.33	86.67	16.00	0.33	61.33	-
840317	26.33	21.00	1.67	2.33	1.33	-
Without carcasss						
840311	4.62	0.69	0.08	0.38	0.15	-
840317	6.31	0.69	0.08	1.23	0.08	-

Table 3.4. Comparison of mean trap abundances of the species for traps next to carcasses and the other traps in the grid.

For all species except *C. hilli* the catches of traps next to carcasses are significantly enhanced. It can also be seen that this enhancement decreases from the first trapping day (when the carcass was fresh) to the next trap day a week later. This trend is not reflected in the other treatment (traps without carcasses) and so discounts the effect of changes in general fly abundance from one trapping day to the next.

If it can be assumed that the majority of *L. cuprina* visiting the fresh carcass are doing so in order to lay eggs [a view supported by the work of Woodburn & Vogt (1982)] then it follows that the ensuing larvae are not successfully completing their development. Any interference in their development would have to be dramatic as no emerging *L. cuprina* were recovered even though the emergence tents were designed to optimise their capture.

This experiment is in no way conclusive in demonstrating a competitive influence between the species in the field. It is evident from the emergence records that *Ch. rufifacies* is the dominant species emerging from these carcasses and the outcomes in its absence as given below are interesting for comparison.

3.2.3.2 Competition in the absence of *Chrysomya*

The emergence records for this experiment are given in Table 3.5(a-c). Once again the catches from traps set adjacent to the carcasses for the interval between the time at which they were placed in the field and the time at which first emergences were recorded are included. The sites at which the carcasses were deposited were the same as for the previous year.

Date	<i>L.c</i>	<i>L.s</i>	Species <i>C.s</i>	<i>C.h</i>	<i>Ch.r</i>	<i>Ch.v</i>
Trap data						
850119	45	18	7	1	-	-
850126	21	16	2	1	-	-
Emergence data						
850209	1	6	14	-	-	-
850216	-	101	3	-	-	-
850223	-	15	-	-	-	-
Total emerging	1	122	17	-	-	-

Table 3.5a. Emergence and trap records by date and species for Carcass 1.

Date	<i>L.c</i>	<i>L.s</i>	Species <i>C.s</i>	<i>C.h</i>	<i>Ch.r</i>	<i>Ch.v</i>
Trap data						
850119	68	42	21	1	-	-
850126	19	17	9	-	-	-
Emergence data						
850209	-	-	-	-	-	-
850216	2	16	353	-	-	-
850223	-	2	2	-	-	-
Total emerging	2	18	355	-	-	-

Table 3.5b. Emergence and trap records by date and species for Carcass 2.

Date	<i>L.c</i>	<i>L.s</i>	Species <i>C.s</i>	<i>C.h</i>	<i>Ch.r</i>	<i>Ch.v</i>
Trap data						
850119	32	63	47	-	-	-
850126	12	29	18	-	-	-
Emergence data						
850209	-	-	6	-	-	-
850216	49	32	84	-	-	-
850223	12	14	5	-	-	-
Total emerging	61	46	95	-	-	-

Table 3.5c. Emergence and trap records by date and species for Carcass 3.

As was seen in the section above the abundance of species trapped bears no relation to the subsequent emergences. However, with the exception of *C. hilli*, all the species recorded visiting the fresh carcasses are also found amongst the species emerging. Once again a clear enhancement of trap catches can be seen for traps in close proximity to carcasses, with only *C. hilli* catches relatively unaffected (Table 3.6). The decrease from the first trapping day to the next trap day a week later is also repeated.

Date	<i>L.c</i>	<i>L.s</i>	Species <i>C.s</i>	<i>C.h</i>	<i>Ch.r</i>	<i>Ch.v</i>
With carcasses						
840311	48.33	41.00	25.00	0.67	-	-
840317	17.32	20.67	13.00	0.33	-	-
Without carcasses						
840311	1.92	3.46	1.67	0.08	-	-
840317	5.00	3.77	1.87	0.38	-	-

Table 3.6. Comparison of mean trap abundances of the species for traps next to carcasses and the other traps in the grid.

The species mix emerging from these carcasses is quite different from the outcome

of the previous experiment. *L. sericata* is present in larger proportions and *L. cuprina* is seen emerging in significant numbers from Carcass 3. Even though the emergence tents were not designed for *C. stygia* they represent the most numerous species in the samples.

3.2.3.3 Temperature history of the carcass

The temperatures measured from Carcass 1 in the 1983-84 summer season are given in Table 3.7. The temperature probes are annotated as in Figure 3.5. Also included in this Table are mean values for the thermistor probes in the outer surface of the carcass and for probes in the lower layer closer to the ground.

A graphical presentation of the ambient, core, mean upper (U) and lower (L) layer carcass temperatures is given in Figure 3.9. From this graph it can be seen that carcass temperatures are rarely lower than ambient temperatures. Up to 72 hours *post mortem* the carcass temperatures are largely dependent on ambient temperature. However, after this time the core temperature becomes independent of ambient and the mean U and L temperatures become less affected by diurnal variation in ambient temperature. Peak temperatures of 40°C are reached at this time by the core temperature and sustained intermittently for a period of 48 - 60 hours after.

At around 144 hours *post mortem* the core temperature starts to be governed by ambient temperature whilst mean L become more independent. It is also at this time that the greatest differential temperature is seen between mean U and ambient temperatures. By 192 hours *post mortem* the core temperature starts to drop rapidly and by 240 hours all temperatures are following the diurnal variation in ambient temperature.

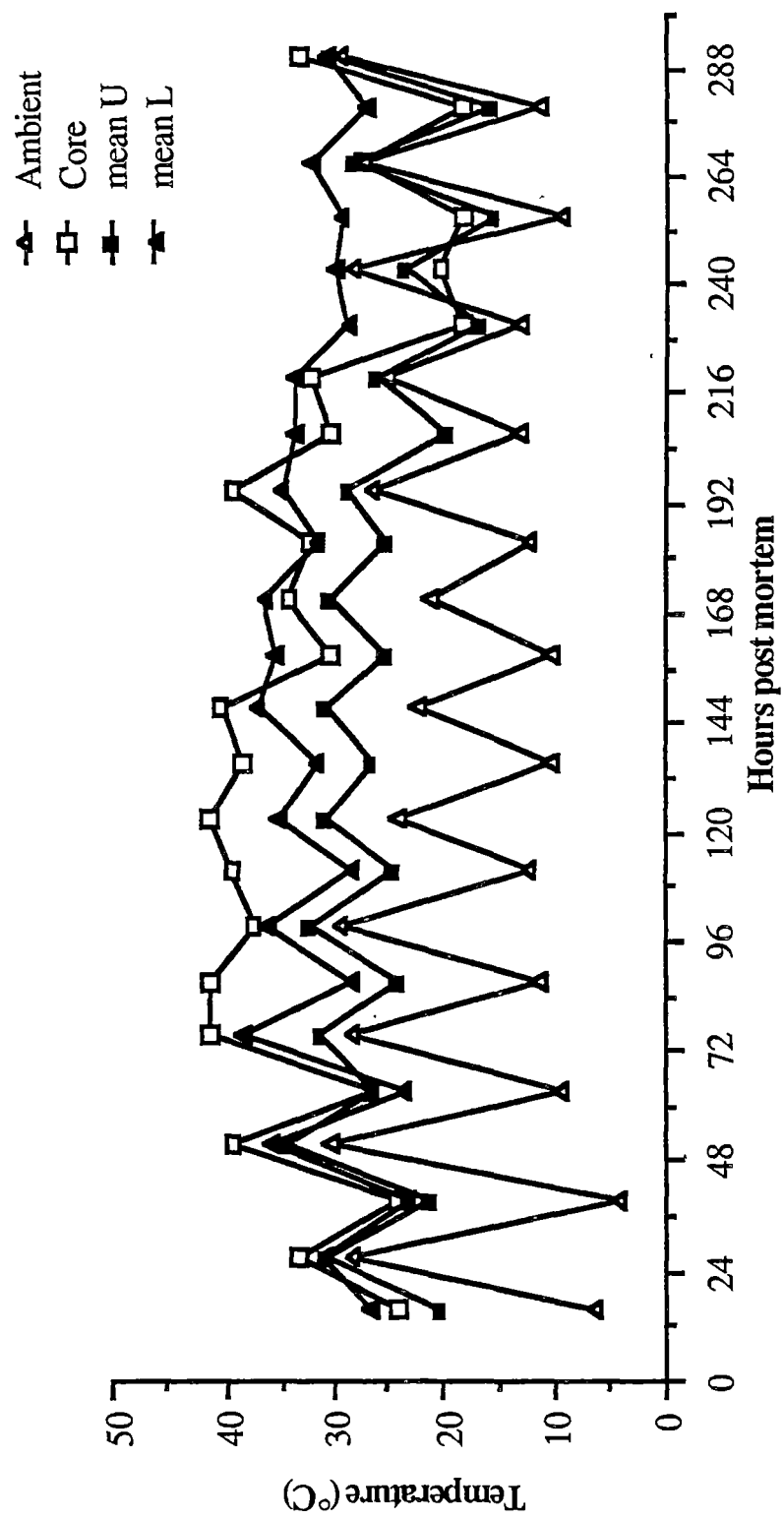


Figure 3.9. Temperature records from the sheep carcass for the first 300 hours after death.

Hours post mortem	Ambient	Mean		CORE	Temperature probe and reading (°C)															
		U	L		U1	U2	U3	U4	U5	U6	U7	U8	L1	L2	L3	L4	L5	L6	L7	L8
12	5	18.9	25.4	23	22	16	18	20	18	20	19	18	25	24	27	26	25	26	25	25
24	27	29.4	29.8	32	29	30	28	31	30	31	26	30	23	30	29	30	30	33	31	32
36	3	20.1	22.0	23	19	11	21	20	23	24	20	23	18	21	25	27	20	21	20	24
48	29	32.9	34.4	38	35	31	31	32	37	33	32	32	32	35	32	33	36	38	32	37
60	8	25.0	22.3	25	23	18	26	24	26	30	25	28	21	22	23	22	21	23	22	24
72	27	29.9	37.0	40	35	32	32	31	36	20	33	20	37	38	35	36	33	40	39	38
84	10	23.0	27.0	40	33	24	25	23	18	19	24	18	28	26	21	20	29	33	29	30
96	28	30.9	34.9	36	29	30	29	31	32	33	31	32	28	32	34	32	36	40	38	39
108	11	23.1	27.0	38	17	26	24	21	24	24	27	22	21	29	23	21	27	35	28	32
120	23	29.3	33.8	40	27	32	28	29	27	32	28	31	38	40	29	27	29	40	32	35
132	9	25.3	30.4	37	22	28	23	22	18	19	35	35	35	38	21	18	25	40	31	35
144	21	29.5	35.8	39	25	33	28	25	25	29	35	36	36	40	32	34	28	40	40	36
156	9	24.0	34.3	29	18	22	21	20	20	18	40	33	33	40	23	40	22	38	40	38
168	20	28.9	35.1	33	24	25	24	25	24	34	40	34	25	37	33	40	29	40	40	37
180	11	23.9	30.4	31	26	23	20	20	18	16	38	30	18	32	19	40	20	36	40	38
192	25	27.5	33.6	38	28	27	27	28	26	28	27	31	29	29	29	32	34	40	40	36
204	12	18.3	32.1	29	30	15	23	21	13	15	14	15	32	19	24	25	38	40	40	39
216	24	24.8	32.4	31	33	24	24	22	24	22	25	24	33	27	26	23	37	40	35	38
228	12	15.4	27.4	17	19	13	14	20	12	12	15	18	23	18	18	21	37	37	29	36
240	27	22.4	28.7	19	21	25	16	20	28	15	29	27	25	25	19	23	37	37	31	32
252	8	14.1	28.0	17	19	13	14	19	14	12	10	12	22	21	17	22	38	36	29	33
264	26	26.9	31.0	26	27	26	24	23	28	27	30	30	26	28	26	25	37	38	29	39
276	10	14.6	25.7	17	19	14	13	16	11	12	13	14	21	19	18	19	38	31	21	38
288	28	28.9	29.3	32	29	22	29	27	30	33	32	28	25	26	30	27	35	31	28	32

Table 3.7. Temperature probe recordings of ambient and carcass temperatures for Carcass 1.

3.3 DISCUSSION

3.3.1 SEASONAL AND GEOGRAPHIC DISTRIBUTION

The species composition and distribution recorded during this study differ markedly from those of other studies. The only Tasmanian study of blowfly distribution, by Ryan (1954), does not record the presence of *Chrysomya rufifacies* or *Chrysomya varipes*. The presence of *Ch. rufifacies* at Ross reported here represents the southernmost record of this species. The discovery of *Ch. rufifacies* and *Ch. varipes* in Tasmania was made simultaneously during this study and another at the Tasmanian Department of Agriculture, and reported in McQuillan, Jones and Williams (1983).

The contrasting distribution of *Lucilia sericata* in Tasmania compared with that of the mainland of Australia has been reported by Ryan (1954) and is supported by this work. The Joint Blowfly Committee (1933) noted that *L. sericata* had a mainly coastal distribution. This general distribution was refined further by Waterhouse and Paramonov (1950) who also found a degree of mutual exclusion between the distributions of *L. sericata* and *L. cuprina*. They found that the distribution of *L. cuprina* was restricted to semi-arid conditions and was mainly related to sheep distribution. In contrast *L. sericata* was common in habitats which were generally closely settled and had a high humidity. The distribution of this species was not correlated to the distribution of sheep. Nicholson (1934) reported that *L. sericata* and *L. cuprina* were often found together but that *L. cuprina* was mainly found in warm regions and *L. sericata* in cooler areas. More recently, Vogt and Woodburn (1979) concluded that *L. sericata* was poorly represented in rural areas.

Tasmania is on the whole more closely settled than rural areas of the mainland and this may account for the high proportion of *L. sericata* caught during this study. However, during the course of the field work all the areas trapped were in severe drought and so it

would seem that the humidity factor is unimportant to the distribution of *L. sericata*.

For species other than *Chrysomya* the seasonal trends generally agree with those reported by Barton (1981) for flies in Victoria. He found that the *Calliphora* spp. peaked in late spring to early summer and that their numbers gradually declined to the end of the season (March- April). Of the *Lucilia* spp. caught, *L. sericata* represented 2.25% of the catch. In contrast to the present study Barton (1981) found that *Ch. rufifacies* appeared in November and their abundance peaked in January, coinciding with the peak in *Lucilia* spp. abundance.

The earlier appearance of *Ch. rufifacies* in Victoria and the apparent correlation of its abundance with that of *Musca vetustissima* (McQuillan pers. comm.) suggest that this species is migratory with no permanent population in Tasmania. Southward migrations of *M. vetustissima* have been noted (Hughes, 1970; Hughes and Nicholas, 1974) and are associated with anticyclonic systems occurring over south eastern Australia in summer. These systems have been shown to be related to insect migration over Bass Strait (Drake *et. al.* 1981). Further evidence for immigration and a gradual southward movement through Tasmania is given in this study by the sequential first occurrence of *Ch. rufifacies* along the north south trapping transect. The earliest occurrence is at the most northerly site, whilst the latest occurrence is at the most southerly site.

The large difference seen here between densities of *L. cuprina* at different trapping areas is a phenomenon noted by Norris (1959).

3.3.2 SPATIAL INTERACTION

Norris (1959), reported that microgeographical variation within a habitat effects the density of flies. Vogt and Woodburn (1979) found that there was great variation in

local densities of *L. cuprina*, whilst the relative densities of flies at different sites remained much the same throughout a season. This conclusion is supported by Wardhaugh *et al.* (1983a) who found a highly contagious and persistent distribution for *L. cuprina* in a field release of flies. In general they concluded that the habitats where flies were either abundant or infrequently caught tended to remain the same through the season. The present study also reports a contagious distribution for *L. cuprina* and a seasonally fixed local pattern of relative abundance.

The stable local distribution of *L. cuprina* probably points to a sedentary habit in this species. That is, if dispersal was great a more random distribution should be found and the apparent pattern of abundance would also change through the season. Gurney and Woodhill (1926) report that *L. sericata* [probably *L. cuprina* misidentified] were very localised, staying within 1-2 miles of the liberation point in a field release experiment. This was also reported by Norris (1959) and Barton (1981) who report that *L. cuprina* were very localised, travelling an average of 1 mile and 1-2 km respectively.

From a study of the energetics of dipterans Roff (1977) concluded that dispersal was energy expensive with the major compromise for the allocation of resources being between flight and reproduction. In a comparative study of the energetics of the various components of the Tasmanian necrophagous fly guild Williams and Richardson (1983) found that *L. cuprina* allocated the highest proportion of its resources (on a somatic weight basis) to egg production. They concluded that *L. cuprina* should be the most sedentary of the species. Furthermore they found that there was a higher commitment to egg production in smaller forms of *L. cuprina* and suggested that this would result in a proportional decrease in dispersion with size.

The strong correlation between the distribution of *L. cuprina* and live sheep.

reported here supports the observations of Vogt and Woodburn (1979) who suggested that there was a correlation of fly abundance with the presence/absence of sheep.

3.3.3 CARRION EXPERIMENTS

The results of the present study shows that under some conditions *L. cuprina* may emerge from carrion in varying numbers. It is impossible to quantify the level of breeding in carrion which could be considered as significant for *L. cuprina*. However, as this species is capable of producing a large number of offspring from a single female the importance of a low level population breeding through carrion in the absence of myiasis should not be discounted.

Norris (1965) noted that predictable outcomes from carrion were not possible due to the number of variables affecting growth and survival. In an extension to this Hanski (1977) found that the timing and order of arrival of species at a carcass is of great importance to the eventual outcome amongst the competing larvae. Waterhouse (1947) recorded a mean emergence of 4 individuals of *L. cuprina* from carrion (with a range of 0-915). This demonstrates the patchy success rate of this species in carrion also seen in the present study. He also found that the intense competition encountered in carrion resulted in many larvae leaving at reduced sizes and that a proportion of these wandering larvae failed to pupate. This phenomenon and its implications to the field population of flies is the subject of the following Chapters.

The effects of predation in limiting the survival of blowfly larvae in carrion have been covered at length in the literature. Whilst Anon (1930) notes that *Lucilia* spp. are the first species to arrive at carrion and oviposit, the numbers of their larvae are reduced by *Chrysomya* spp., *Mormoniella* spp. and Staphylinidae. This point is supported by the later work of Fuller (1934) who elevated the role of *Ch. rufifacies* to that of the principal

predator and also suggested the production of a repellent by this species which drove the primary maggots from the carcass. Waterhouse (1947) also found that the reduction in numbers of *L. cuprina* larvae in summer was due to *Ch. rufifacies*. However, he suggested that *Ch. rufifacies* did not exclude larvae from carcasses by the production of a repellent but rather by producing temperatures above the thermal tolerance of the primary fly larvae.

Waterhouse (1947) found that many larvae of *L. cuprina* were killed by high temperatures in carcasses. He inferred that these high temperatures were generated by *Ch. rufifacies*. As well as the high mortality encountered whilst feeding in carrion he estimated a mortality rate of 98% for larval *L. cuprina* leaving the carcass and being preyed upon by *Ch. rufifacies*. The observation that *Ch. rufifacies* will not oviposit at a carcass until other larvae are present (Norris, 1959) supports the role of this species as an active predator of other blowfly larvae.

Barton (1981) working in Victoria found that all sheep blowflies prefer to oviposit on carrion when available. He found that the major species emerging from carrion were *C. stygia* in spring, and *Ch. rufifacies* in summer. Because *Ch. rufifacies* was not abundant in Victoria he reasoned that the general assumption that *L. cuprina* is suppressed by *Ch. rufifacies* did not necessarily hold. He concluded however, that with the exception of late season carcasses (ie. in April) carrion was of little importance as a breeding site to *L. cuprina*.

Ch. rufifacies is not the only species implicated in the reduction of *L. cuprina* larvae in carrion. The Joint Blowfly Committee (1933) noted that *Calliphora* spp. reduced the numbers of *Lucilia* spp. in carrion by competition. Mackerras (1936) found that there was generally intense competition in carrion and this led to the *Lucilia* spp. suffering from

competition from the *Calliphora* spp. and predation from *Ch. rufifacies*. Waterhouse (1947) found that in spring and autumn competition from *Calliphora augur* was an important factor in the reduction of *L. cuprina* numbers in carrion. McQuillan *et.al.* (1983) found that *Calliphora* spp. were always present in carrion in Tasmania. They also found that *Lucilia* spp. could be found in carcasses when *Ch. rufifacies* larvae were absent.

The role of temperature in affecting the success of *L. cuprina* has been mentioned above. Waterhouse (1947) measured the core temperature of a sheep carcass for 18 days after death. As in this study he found that the core temperature soon became independent of ambient air temperature, a phenomenon also noted by Payne (1965). Maximum temperatures in the range of 40-45°C were recorded. Whilst peripheral temperatures were not measured he noted that the temperature should vary in different regions of the body, depending on the rate of heat loss and the size and distribution of larvae.

His measurements were made in winter and in the absence of *Ch. rufifacies*, he therefore postulated that higher carcass temperatures would be encountered in summer. This is not supported by the present study which employed a carcass exposed in summer and infested with *Ch. rufifacies*. Williams and Richardson (1984) suggested that in the absence of *Ch. rufifacies*, *L. cuprina* should be the best adapted fly species in the Tasmanian guild in terms of temperature tolerance to exploit carrion, its upper thermal tolerance being higher than that of the other species. Levot *et. al.* (1979) used the point of most rapid growth in larval development to measure success in competition and concluded that *L. cuprina* was advantaged over *Ch. rufifacies* and *C. stygia*. However their experiments were only conducted over a temperature range of 27-28 °C and so did not take account of thermal tolerances.

The possibility that *L. cuprina* breeds in carrion has been suggested in the

literature (Fuller, 1934; Kitching, 1981). Holdaway (1932) advances the hypothesis that with the introduction of *L. cuprina* to Australia there was shift away from its original carrion habit to that of myiasis. Zumpt (1965) noted that *L. cuprina* larvae could feed on both live and dead tissues, a factor supporting Holdaway's idea of a generalist swapping from one type of resource to another. Zumpt (1965) also noted that *L. sericata* only fed on dead tissue. This observation is not supported by Australian evidence of the occurrence of this species in myiasis in Tasmania (Watts *et. al.*, 1976).

Supporting Holdaway's idea is the wide variation in habit with geographic distribution that can be seen for the *Lucilia spp.*. Fuller (1934) found that both *L. cuprina* and *L. sericata* breed in carrion on the Australian mainland. In Britain, Cragg (1955) found that *L. sericata* was only important in carrion when the larval infestation was present before death. In North America, Denno and Cothran (1975) found *L. sericata* to be a primary fly in carrion in early spring. The *Lucilia spp.* are considered to be the best adapted of the South African guild to competition in carrion with *L. sericata* being a commonly reared species from carrion in winter (Ullyett, 1950).

The importance of carrion as a breeding site of *L. cuprina* may be underrated. Barton-Browne *et al.* (1976) concluded that the primary importance of carrion to *L. cuprina* was for breeding, the males being sexually stimulated by carrion odours. The strong attraction of carrion to *L. cuprina* found by Woodburn and Vogt (1982) was also attributed to concentration of flies for mating rather than for breeding. This was supported by the observation that live sheep attracted mainly females, whilst carcasses attracted both males and females. The fact that oviposition occurred as a result of attraction to carcasses in the latter study was not accounted for.

3.4 CONCLUSIONS

- (i). *Chrysomya rufifacies* and *Chrysomya varipes* are recorded from Tasmania with the southernmost record of *Ch. rufifacies* being at Ross.
- (ii). *Lucilia sericata* forms a significant proportion of the trap catches at all sites.
- (iii). *Lucilia cuprina* has a generally contagious distribution, with weak negative interaction resulting in strong nodes of abundance within the trapping grid. *L. sericata* exhibits a similar distribution but with stronger clumping.
- (iv). *L. cuprina* shows a strong positive correlation to sheep distribution.
- (v). All the species show a positive correlation of varying degree to carrion.
- (vi). No relationship is seen between species abundance at trap sites and emergence from carrion.
- (vii). When *Ch. rufifacies* larvae are present they dominate the flies emerging from carrion, and few if any *L. cuprina* emerge.
- (viii). In the absence of *Ch. rufifacies* the emergence of *L. cuprina* is stronger from carrion.
- (ix). Peak core temperatures of 40°C were measured from an experimental carcass infested with *Ch. rufifacies*.
- (x). Core temperatures are relatively independent of ambient temperature compared to

peripheral temperatures of the carcass.

CHAPTER 4.

INTRA-SPECIFIC EFFECTS OF COMPETITION IN CONTROLLED SIMULATIONS OF CARRION AND MYIASIS.

4.0 INTRODUCTION

The common occurrence of competition for food during the larval stage of blowflies has been discussed in previous sections. The effect of larval food shortages on mortality is reduced by the ability of larvae to complete the feeding stage at sizes below the optimum (Putman, 1977). They are thus able to pass from the feeding stage without having to grow to an optimum size and pass onto the subsequent developmental stages. The proportion of the maximum larval size at which they can successfully proceed through their development varies for the different species.

A consequence of reduced size at pupation is the reduced size of the emerging adult. These small adults (also referred to as 'fractional adults') are capable of dispersal and reproduction. However, basic changes may occur in the relative allocation of energy to the different functions (Roff, 1977; Williams and Richardson, 1983).

Collins (1980) conducted an analysis of phenotypic plasticity in insects. The ability of blowfly larvae to pupate at a wide range of sizes was one phenotypic characteristic which he examined. His analysis was based on the following reasoning- '*the degree to which a life history feature deteriorates in response to realistically applied, naturally occurring stresses should be an inverse of the importance of that parameter to fitness*'. He noted that limited larval food resulted in reduced adult size, fecundity and development time, but that prereproductive mortality was moderated. Due to the high degree of this response in blowflies he concluded that adult size was relatively unimportant

whilst the risk of mortality in the late larval stage was the most critical factor affecting the fitness of blowfly populations.

In an extension to this argument the idea of an optimal size has been challenged. Rather, it has been suggested that the range in variation of a phenotype may have evolved as an optimal solution to the challenges of an unpredictable environment (Kaplan and Cooper, 1984).

The relationships between larval size and some adult characteristics of *Lucilia cuprina* have been studied. Nicholson (1950) found that with increasing larval competition mortality increased only slightly with decreasing pupal sizes. A critical point was reached where mortality increased dramatically. He concluded that the implication of this for the control of *L. cuprina* was that merely killing a large proportion of a field population would not necessarily reduce their long term abundance. The inference here is that the increased survival gained by a sacrifice in adult size is a reflection of the importance of persistence to this organism. The persistence of a very few individuals, given their high fecundity, is an adaptive strategy for an opportunistic species. The persistence of *Musca vetustissima* in poor conditions has been attributed to the interplay between mortality and the relatively higher fecundity of small adult flies (Hughes, 1977a).

Given that competition is an important variable in the larval habitat, the degree of competition in different habitats should be considered. It is generally accepted that competition in carrion is more intense than that occurring in myiasis (Waterhouse, 1947; Norris, 1965). If these different levels of competition occur consistently in the field then the size distribution of flies from a field sample should reflect their original larval habitats. That is, small forms would be produced from flies breeding in carrion and larger forms from myiasis. It is unlikely that competitive levels would be consistent with this model

since the determinants of size distributions are probably much more complex. However, the basic principle is interesting and worth pursuing as it will be in Chapter 5.

Before work of that nature can be done the effects of changes in adult size need to be examined, as does the proposal that competitive levels vary in different larval habitats. To this end this Chapter seeks to determine if there is a predictable outcome to a given level of intra-specific competition. The effect of competition on other life history characteristics such as rate of reproductive development and mortality will also be examined as will the relative differences between competition in the two different larval habitats of *L. cuprina*.

4.1 METHODS

4.1.1 GENERAL CULTURE TECHNIQUES

4.1.1.1 Adult cultures

Adult cultures were maintained from wild stock caught at Ross. Field trapped flies were anaesthetised with CO₂ gas, and sorted by species and sex. Females of *L. cuprina* and *L. sericata* were placed in separate adult holding cages with water, sugar and approximately 10 g of MRM (described in Sect. 4.1.1.2) on a petri dish. The MRM was examined frequently until several egg clusters were visible. At this time the medium was removed from the cage and the eggs were allowed to hatch. After hatching the MRM and first instar larvae were removed from the petri dish and placed onto a larger quantity of MRM (usually approximately 500 g). These larvae were cultured in the same containers as for the experiments described below, and at 20°C, 70% RH (relative humidity) and 12h:12h light/dark. After pupation the pupae were removed from the rearing trays and placed in adult holding cages.

Emerging adults were fed water, sugar and protein (in the form of MRM) *ad libitum*. Eggs from these cultures were treated as above until the stock had a pedigree of at least 5 generations of laboratory reared flies. At this time the eggs produced were used for the experiments described below. The stocks were replenished after every second egg laying cycle had finished.

This method and the controlled conditions worked very well for *L. cuprina*. The cultures behaved predictably and there was never a problem with a shortage of eggs. However, cultures of *L. sericata* were impossible to maintain. Oviposition on the MRM was erratic and the eggs were usually infertile. Mating was rarely observed in the adult cultures and this was seen as the major problem with the technique. Lighting conditions were changed to give near natural light conditions from fluorescent tubes and different

protein substrates such as whole meat, liver and mouse carcasses were tried as alternative oviposition sites. Despite these changes no change was seen in the number or fertility of eggs produced. Due to the low number of egg clusters successfully hatching, subsequent cultures were inbred and too small to be viable. Because of these difficulties experiments planned for *L. sericata* were abandoned.

4.1.1.2 Larval cultures

In the experiments described below and the larval cultures required to sustain the adult stocks, the larval medium referred to is that of the CSIRO larval mass rearing medium (MRM). This is prepared by mincing liver, water and cotton linters in the ratio 16:5:1.5 by weight. One batch of 200 kgs MRM was made for this work. To avoid contamination by pesticides the liver used was from dairy cows, the cotton linters were kindly provided by CSIRO Division of Entomology and were also pesticide free.

The culture medium and larvae were placed on polystyrene meat packing trays (Snowpak No. 87) over about 2-3 cm of Grade 1 vermiculite. The vermiculite (which acted as a pupating medium) was stored at 80% RH prior to use. The culture boxes were a Decor 254 with fine stainless steel mesh welded into the lid. This allowed for a free movement of air, and also prevented contamination by parasitoids and the escape of wandering larvae.

Cultures were prepared by weighing out amounts of MRM. A sample of MRM from each batch of trials was retained and dried in a vacuum oven at 60°C to determine dry weight. This was then used to standardise the weight of culture medium for any variation in water content which may have occurred between the batches.

Larvae were transferred to the prepared medium at approximately 4 hours after

hatching. They were transferred at this stage because they seemed robust and were still concentrated around the original egg cluster. This made them easier to count out accurately. The method was also successfully employed by MacLeod (1937).

After this preparation the culture boxes were left in the required conditions of temperature and humidity. Whilst they were inspected at least once every day, care was taken not to interfere with them physically. Signs that the larvae had reached the wandering stage could be seen when the MRM was either excessively disrupted or partly buried in vermiculite. At this point the culture boxes were inspected through their clear bases. The wandering larvae buried in the vermiculite could be seen in this manner.

When a high proportion of the larvae had pupated, the boxes were unsealed and the used MRM and polystyrene tray were removed. Larvae or pupae remaining in the MRM were returned to the remaining vermiculite. The vermiculite was then passed through a 2 mm mesh sieve and the pupae, quiescent larvae and wandering larvae were counted and retained. These were then treated as outlined in the preceding section in preparation for emergence.

4.1.2. ARTIFICIAL CARRION EXPERIMENTS

4.1.2.1 Changes in life history parameters with varying competition regimes and temperature

In this experiment the initial number of first instar larvae on a fixed quantity of MRM was varied. The cultures were prepared as outlined in the preceding section. To minimise the number of cultures used, a preliminary experiment examined the range of densities of larvae on MRM which would yield adults at the extremes of possible sizes. When this experiment was completed subsequent culture densities were restricted to those known to produce adults, and were repeated for a range of temperatures. This experiment

was also used to determine changes in ovariole number with adult size.

a. Preliminary experiments

1. Determining the feeding regimes.

For this pilot experiment a range of densities of 2-120 larvae per gram of MRM were used. These cultures were reared at 20°C and 80±10%RH. After pupation the number of pupae were noted, and then reared through to emergence. No food was supplied to the emerging adults. Dead flies were removed to storage in alcohol until no more flies were left in the culture.

All flies from these samples were then sexed, counted and the thorax length measured. In this and all following sections thorax length measurements refer to the distance (in millimetres) between the base of the cervical sclerites lying laterally adjacent to the neck on the prothorax, to the posterior extreme of the scutellum. This measurement was chosen as it involved less handling than similar measurements such as head width.

2. Changes in ovariole number.

Female flies representative of the range of sizes collected in the samples described above were measured (thorax length) and their ovaries dissected. The method used to stain the ovarioles is that of Vogt *et. al.* (1974). The dissected ovaries were soaked in insect Ringer's solution for 2 minutes, and then stained in a filtered preparation of 1 g neutral red in 100 ml insect Ringer's solution.

The ovaries were stained for 30 seconds and then washed in insect Ringer's and placed separately on a slide. They were then teased apart and stretched to expose all the ovarioles and wet mounted in insect Ringer's. The number of ovarioles in both ovaries were counted and the total number recorded.

4.1.2.1.2 Changes in larval mortality and life history parameters with varying competition regimes and temperature

Cultures covering the range of larval densities known to produce adults from optimal sizes to the extreme minimum size were initiated and reared at five different constant temperatures. These were 20°C (80±10%RH), 25°C (80±5%RH), 30°C (80±10%RH), 35°C (85±10%RH) and 40°C (85±5%RH).

The cultures were checked at regular intervals during the day (8.00am to 9.00pm) until the majority of larvae had entered the wandering stage. Because the larvae have a propensity to leave the food source *en masse* (Smith, *et al.*, 1981) this point is well defined. The time at which this stage was observed was noted and after a period allowing the remainder of the larvae to leave the MRM the vermiculite was transferred to a sealable, clear plastic container. Any larvae pupating in the MRM residue were removed to the new container. These containers were checked daily for emergences. Newly emerged flies were sexed and counted, and then transferred to an adult rearing cage where water, sugar and MRM were supplied *ad libitum*.

During the daily checks of the pupal containers, the number and sex of dead flies in the adult rearing cages were also noted. Dead flies were removed from the cages and stored in alcohol. The MRM was replaced daily and the old medium checked for egg clusters. If egg clusters were present, the event was noted.

When all of the emerged adults had died, the contents of the container originally holding the vermiculite and pupae were sieved and any diapausing larvae were removed and counted. The thorax lengths of the adults stored in alcohol were measured.

4.1.3 ARTIFICIAL MYIASIS EXPERIMENTS

The sheep used in these experiments were three Polworth 2-tooth wethers, purchased from the same property and with full fleeces. Between experiments they were kept on pasture. During the experiments they were kept at the University of Tasmania's Medical School Animal House. The animal house had facilities to control the light/dark conditions, and these were set to a 12h:12h cycle. The temperature in the animal house remained at approximately 20°C during the term of the experiments.

For the purpose of the experiments the sheep were placed in elevated cages 1.5 m long by 0.5 m wide. The walls of the cages were 1 m high, and containers for food and water could be attached to them. The floors of the cages were made of weldmesh, with openings large enough to allow faeces to fall through to a finer meshed tray. These trays could be removed for cleaning.

A recurved lip fabricated from sheet metal was fitted around the floor of the whole apparatus to stop wandering larvae from escaping and to guide them into a fibreglass tray fitted below the faeces collector. This tray had a conical shape allowing urine to drain to a central drain hole under which a bucket was placed. During the experiments this tray was filled with vermiculite after fitting a sieve over the drain hole.

The cages were basically the same as those described by Dallwitz (1983), however, the larval collector differed in that it allowed larvae to find suitable pupation sites rather than concentrating them for sampling. It also prevented larvae from being flushed into the urine collectors.

The conditions for artificial myiasis were prepared by bathing an area on the sheep's flank with water. A 15cm long shallow scratch was made in this area and the

whole area then covered and kept damp for two days. Larvae of approximately 4 hours after hatching were then transferred to the wound. A cotton wool wad made damp with water was placed over the wound and the wool closed around it and stapled together to keep the wad in place.

A range of 100 to 6000 larvae per wound was used. When the larvae had completed development and left the host, the tray was removed and left until pupation was observed. The area in which the larvae were feeding was sheared and all areas showing the characteristic staining of myiasis exposed. The area of the strike was then measured by roughly tracing it onto graph paper.

The contents of the tray were then sieved and all pupae and larvae removed. The number of larvae was noted. They were placed in fresh vermiculite and reared as for Section 4.1.2.1.1. When all of the flies had emerged and died, they were removed to storage in alcohol. The thorax length of these flies, their sex and numbers were then recorded.

4.2 RESULTS

4.2.1 ARTIFICIAL CARRION EXPERIMENTS

4.2.1.1 Preliminary experiments

a. Changes in larval mortality and adult size with varying competition regimes

The results for preadult mortality against competitive regime are presented in Table 4.1. The mean thorax length for males and females against competitive regime are given in Figure 4.1.

Initial number larvae/20 g MRM substrate	Number		Mortality from hatch to-		Sex ratio F:M
	Pupae	Adults	Pupae	Emergence	
40	38	38	0.05	0.05	0.88
60	57	55	0.05	0.08	0.82
80	78	68	0.02	0.15	1.19
100	97	95	0.03	0.05	1.11
120	117	112	0.02	0.07	0.77
140	135	131	0.04	0.06	0.87
160	154	149	0.04	0.07	1.19
180	156	148	0.13	0.17	1.24
200	185	181	0.08	0.10	0.97
220	213	194	0.03	0.12	0.81
240	236	210	0.02	0.13	0.74
260	255	253	0.02	0.03	0.99
280	276	254	0.01	0.09	0.87
300	202	193	0.33	0.36	0.90
320	242	239	0.24	0.25	0.91
360	†	274	-	0.24	1.02
400	†	284	-	0.29	1.09
440	†	198	-	0.55	0.94
480	†	321	-	0.33	0.73
520	†	345	-	0.34	0.87
560	†	88	-	0.84	1.00
600	†	298	-	0.50	0.80
800	†	0	-	1.00	-
1600	†	0	-	1.00	-
2400	†	0	-	1.00	-

Table 4.1 Preadult mortality and competitive regimes.

† - numbers not recorded.

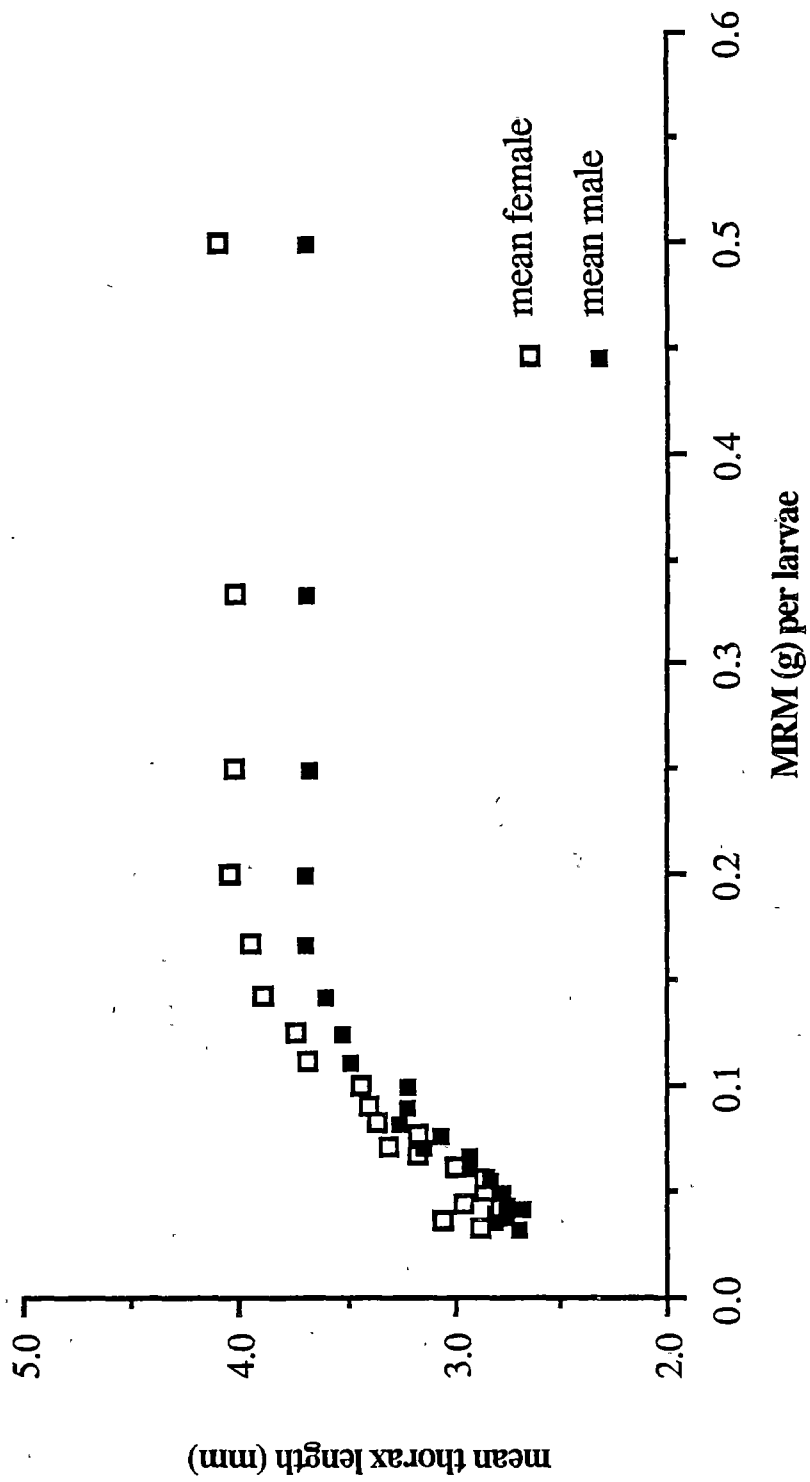


Figure 4.1. Mean thorax length of adults (by sex) reared under different larval densities at 20°C.

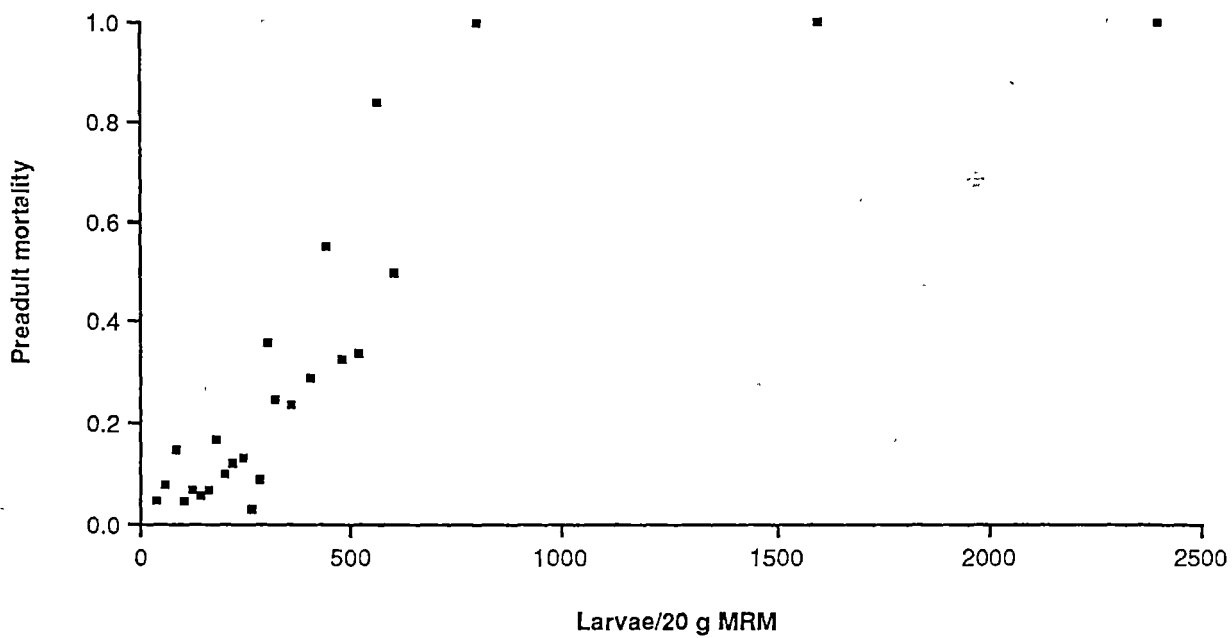


Figure 4.0. Preadult mortality and density at 20°C

From Figure 4.0 it can be seen that preadult mortality generally increases with increasing competitive levels. The increase is not linear but rather increases rapidly from levels of about 300 larvae/20 g MRM. It is at this level that adults reach their minimum size seen in Figure 4.1. The lower mortality levels at competitive regimes below this point are probably due to the compensation of mortality rates by reduction in adult size. As the minimum size is approached with increasing competitive levels the capacity for compensation is diminished and mortality increases.

Male size as measured by thorax length is generally less than that of females. No trend seems apparent in the relationship of sex ratio to competitive levels. As males are smaller than females it could be expected that sex ratios would approach and exceed 1 as competition increases. That is, males by being able to produce adults of smaller size have a greater capacity for compensating mortality.

From this experiment it was decided to use competitive levels of 2 larvae/g MRM, 15-20 larvae/g MRM and 30-40 larvae/g MRM in the series of experiments described below which examined the effects of competition and temperature on mortality and life history characteristics.

b. Changes in ovariole number with adult size

The range in size of female flies examined in this experiment were from 2.0 to 4.4 mm thorax length. A plot of the data and the fitted regression are given in Figure 4.2. An exponential regression was fitted to the data by least square estimation. This gave,

$$N_{Ov} = 23.3636 Tl^{1.6453}$$

$$r_{(2),96}=0.975, SE =0.088, (P<<0.001)$$

where N_{Ov} is the total number of ovarioles for a female of given TI (thorax length in mm). The annotation $r_{(2),n}$ is a two-tailed correlation coefficient with n degrees of freedom ($df=N-2$, where N is the sample size), and SE is the standard error of the regression.

4.2.1.2 Changes in larval mortality and life history parameters with varying competition regimes and temperature

The effects on preadult mortality of competition regime and temperature are shown in Table 4.2. In Figure 4.3(a-c) the relationships of development rates (1/development time) to temperature and competition regime are given for rates of development from hatching to the wandering stage, from wandering to emergence and from emergence to the laying of the first egg clusters. The definition of the time at which the wandering stage commences has been given. The emergence time is taken as the day on which the majority of emergences occurred.

None of the cultures at 40°C produced pupae even though the larvae under the least competitive pressure did complete feeding. Results for this temperature are therefore not given.

From Figure 4.3 it can be seen that development rates for the preadult stages (larval and pharate) are generally higher for larvae under lower competition regimes at the same temperatures. No trend is apparent for development rates through the maturing stage except for the general trend of increasing development rate with temperature for all cultures.

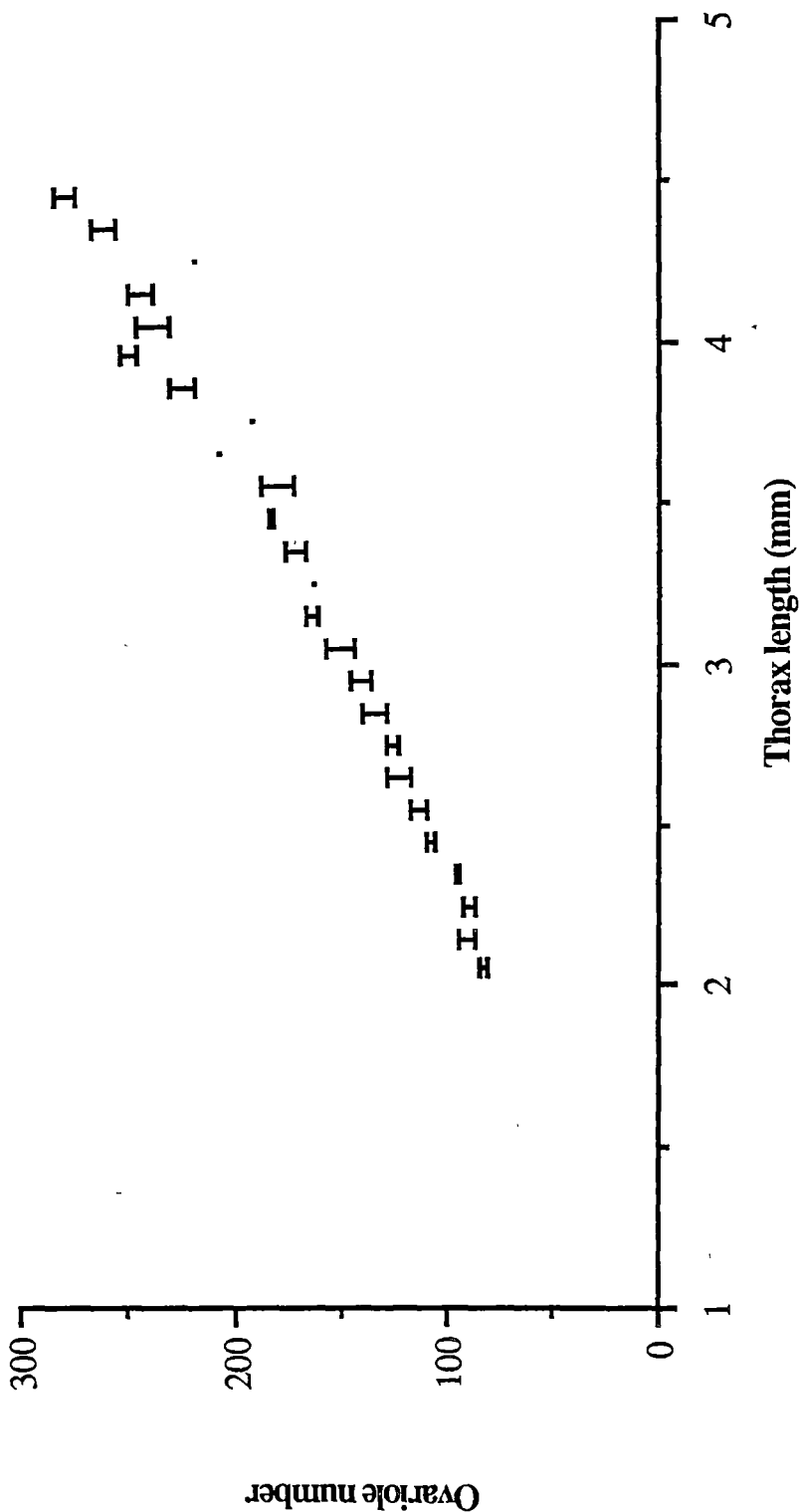


Figure 4.2. The relationship between female thorax length and total ovariole number. Bars represent 1S.E.

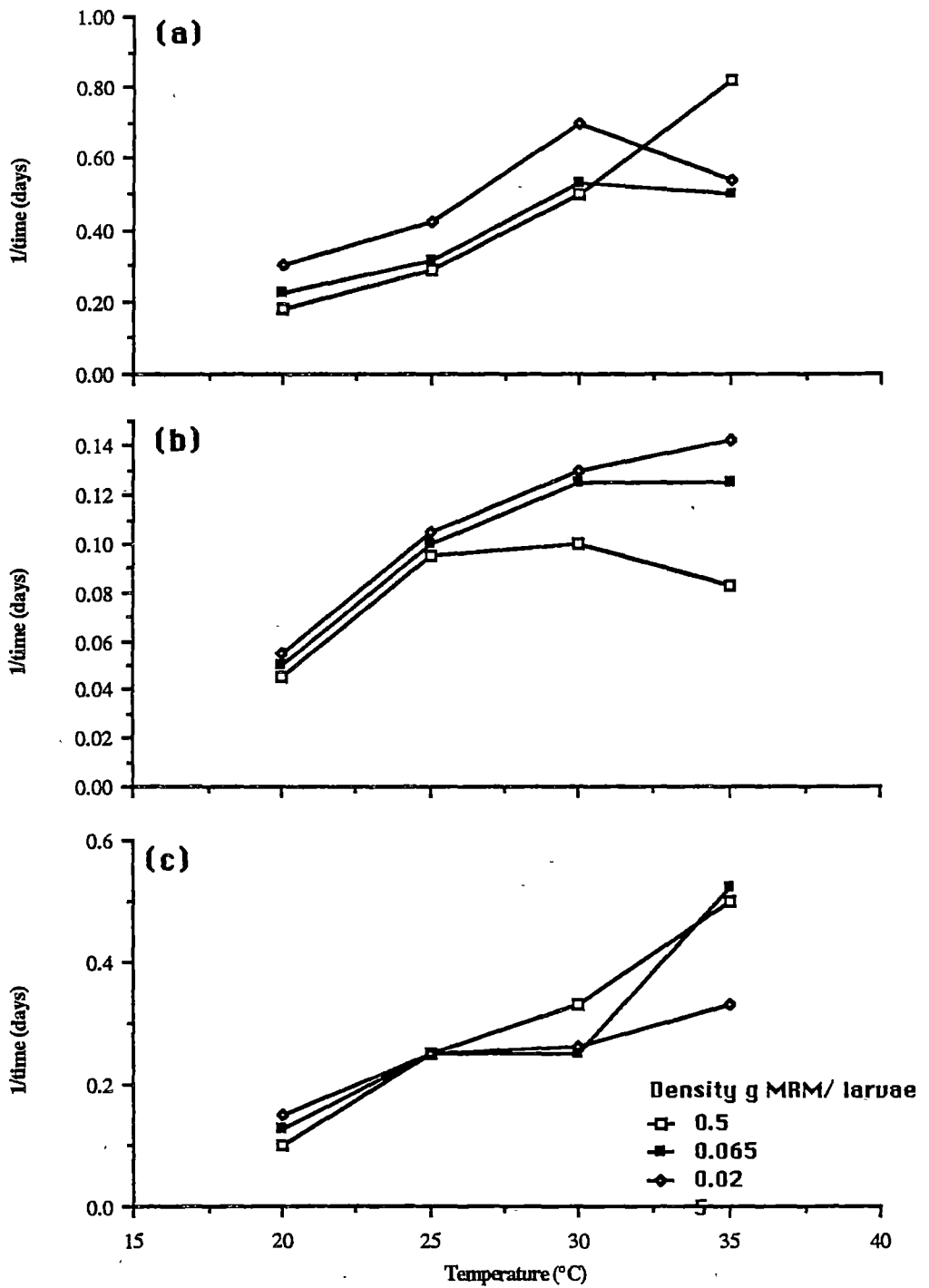


Figure 4.3. Development rates under different larval densities and temperatures. Graphs show development time from (a) egg to wandering stage, (b) wandering stage to emergence, and (c) emergence to the production of the first egg batch.

Temperature (°C)	Density (larvae/g)	Preadult mortality
20	2.0	0.15
	20.0	0.29
	30.0	0.75
	40.0	0.82
	80.0	1.00
25	2.0	0.77
	15.0	0.20
	40.0	0.61
30	2.0	0.70
	15.0	0.11
	40.0	0.67
35	2.0	0.80
	15.0	0.10
	40.0	0.62

Table 4.2. Preadult mortality by larval density and temperature.

The survival of adult flies against time follows a logistic distribution. To linearise this data for further analysis they were transformed to logits before fitting multiple linear regressions for each of the competition regimes and temperatures. The logit transformation takes the following form.

If $S = \Sigma^t$ deaths, [and is standardised to a range of 0 - 1, (where t is time)], and the distribution of S fits the logistic function,

$$S_{(t)} = 1/(1+e^{-(\alpha+\beta t)})$$

then the logit transformation ($S_{(t)l}$) can be applied.

$$S_{(t)l} = \ln(S_{(t)}/1-S_{(t)}) = \alpha + \beta t$$

where α and β are the linear regression parameters for intercept and slope respectively.

Daydegree rates for developmental stages (D°) were calculated for the durations of the larval, pharate, maturing and 50% mortality in males and females. The duration of the

pharate stage is defined here as the time from the start of the wandering stage to the day on which the majority of emergences occurred. The maturing stage is from the time of emergence as defined above to the time at which the first egg clusters were laid.

Daydegrees are calculated as the duration in days multiplied by the temperature ($^{\circ}\text{C}$) at which development occurred. Developmental rates were also calculated for these stages (1/duration in days). The thorax lengths of all flies emerging were measured and the mean size calculated for each sex.

The symbols used in the following analysis are given in the key below.

t = time in days.

T = temperature ($^{\circ}\text{C}$).

C = index of density.
 $(\text{mg substrate DW}_{\text{initial}} - \text{mg substrate DW}_{\text{final}}) / \text{initial number of larvae}$

D°_l = daydegree duration from hatching to wandering stage.

D°_p = daydegree duration from wandering to emergence.

D°_e = daydegree duration from emergence to first egg laying.

D°_{m50} = daydegree duration from emergence to 50% male mortality.

D°_{f50} = daydegree duration from emergence to 50% female mortality.

R_l = rate of development from hatching to wandering stage.

R_p = rate of development from wandering to emergence.

R_e = rate of development from emergence to first egg laying.

R_{m50} = rate of development from emergence to 50% male mortality.

R_{f50} = rate of development from emergence to 50% female mortality.

$S_{(t)lm}$ = logit transformed sum of deaths with time t for males.

$S_{(t)lf}$ = logit transformed sum of deaths with time t for females.

Tl_m = mean thorax length of males.

Tl_f = mean thorax length of females.

SR = sex ratio (female:male)

Multiple linear regressions were fitted to various combinations of these variables with the Statistical Package for Social Sciences (SPSS) regression routine. The results are presented below. Variables are listed in the equations in order of decreasing contribution to the regressions fit, that is the first one describes most of the variation, the next less and so on.

$$D^{\circ}_l = 100.5153 - 2.1822 T + 9.6424 Tl_f \quad [1]$$

$$r_{(2),9} = 0.771, \text{ SE } = 13.250, (0.01 > P > 0.005)$$

$$D^{\circ}_l = 89.0181 - 2.1030 T + 13.3522 Tl_m \quad [2]$$

$$r_{(2),9} = 0.785, \text{ SE } = 12.889, (0.005 > P > 0.002)$$

$$D^{\circ}_e = 257.4993 - 4.9267 T - 2.4359 Tl_f \quad [3]$$

$$r_{(2),9} = 0.766, \text{ SE } = 26.555, (0.01 > P > 0.005)$$

$$D^{\circ}_{f50} = 1576.983 - 38.8959 T + 61.3554 Tl_f \quad [4]$$

$$r_{(2),9} = 0.885, \text{ SE } = 136.120, (P < 0.001)$$

$$D^{\circ}_{m50} = 968.4060 - 20.0923 T + 41.6192 Tl_m \quad [5]$$

$$r_{(2),9} = 0.748, \text{ SE } = 120.061, (0.01 > P > 0.005)$$

$$R_l = -0.1942 + 0.0271 T - 0.0382 Tl_f \quad [6]$$

$$r_{(2),9} = 0.866, \text{ SE } = 0.104, (P < 0.001)$$

$$R_l = -0.1389 + 0.0268 T - 0.0559 Tl_m \quad [7]$$

$$r_{(2),9} = 0.869, \text{ SE } = 0.103, (P < 0.001)$$

$$R_p = 0.0020 + 0.0043 T - 0.0082 Tl_f \quad [8]$$

$$r_{(2),9} = 0.823, \text{ SE } = 0.020, (0.002 > P > 0.001)$$

$$R_p = 0.0083 + 0.0043 T - 0.0103 Tl_m \quad [9]$$

$$r_{(2),9} = 0.823, \text{ SE } = 0.020, (0.002 > P > 0.001)$$

$$R_e = -0.3673 + 0.0202 T + 0.0283 Tl_f \quad [10]$$

$$r_{(2),9} = 0.912, \text{ SE } = 0.058, (P < 0.001)$$

$$R_{f50} = -0.0232 + 0.0047 T - 0.0180 Tl_f \quad [11]$$

$$r_{(2),9} = 0.857, \text{ SE } = 0.020, (P < 0.001)$$

$$R_{m50} = -0.0220 + 0.0043 T - 0.0131 Tl_m \quad [12]$$

$$r_{(2),9} = 0.827, \text{ SE } = 0.020, (0.002 > P > 0.001)$$

Temperature contributes most to describing rates of development in regressions [1] to [12]. Regressions for both D° and R are significant (those for R generally have a higher significance level). The general trend is for increased development rates with temperature and lower competition levels for the range of temperature 20-35°C. The measure of competition level is measured by the thorax length of the ensuing adults.

$$Tl_f = 2.4058 + 0.0296 C + 0.0053 T \quad [13]$$

$$r_{(2),9} = 0.852, \text{ SE } = 0.343, (P < 0.001)$$

$$Tl_m = 2.5060 + 0.0236 C + [0.0000 T \text{ ie. not significant}] \quad [14]$$

$$r_{(2),9} = 0.842, \text{ SE } = 0.271, (0.002 > P > 0.001)$$

$$Tl_f = -0.4923 + 1.2210 Tl_m \quad [15]$$

$$r_{(2),10} = 0.990, \text{ SE } = 0.087, (P < < 0.001)$$

$$Tl_m = 0.4520 + 0.8030 Tl_f \quad [16]$$

$$r_{(2),10} = 0.990, \text{ SE } = 0.070, (P < < 0.001)$$

From regression [13] and [14] it can be seen that the consumption of food in the larval stage contributes most to adult size (as would be expected), whilst temperature has little effect. A simple relationship occurs between female and male adult size from a given level of competition, with females being larger than males.

$$S_{(t)f} = -8.1285 + 0.0761 t + 0.2362 T - 0.1559 Tl_f \quad [17]$$

$$r_{(2),600} = 0.847, \text{ SE } = 1.101, (P < < 0.001)$$

$$S_{(t)m} = -8.2352 + 0.1427 t + 0.2568 T - 0.5274 Tl_m \quad [18]$$

$$r_{(2),352} = 0.828, \text{ SE } = 1.267, (P < < 0.001)$$

Time, temperature and adult size contribute to describing the survival of adult flies described as logits. The highly significant regressions demonstrate that logits describe adult mortality well. Adult mortality increases with age and temperature. The size of adults is inversely proportional to mortality with smaller adults having greater mortalities at the same temperatures.

$$SR = -1.9241 + 0.7562 Tl_f + 0.0278 T \quad [19]$$

$$r_{(2),9} = 0.791, \text{ SE } = 0.392, (0.005 > P > 0.002)$$

$$SR = -2.3138 + 0.8912 TI_m + 0.0318 T \quad [20]$$

$$r_{(2),9} = 0.753, SE = 0.423, (0.01 > P > 0.005)$$

The higher the competition levels the smaller is **SR**. This translates to a higher proportion of males than females as thorax length is decreased. The strength of the relationship shown here contrasts to the lack of an apparent trend in the data presented in Table 4.1. With increased temperature female survival is slightly increased, and with increased density male survival is greater than that of females.

The variation in thorax length and the spread of the thorax length distribution is given in Table 4.3 for the different larval densities and temperatures. It can be seen that as thorax length decreases so does the standard deviation (SD). This relationship can be seen better in Figures 4.4(a-d) where the actual length distributions are presented. At the extreme levels of competition the distributions become skewed to the right. This is probably due to larvae being too small to form viable pupae. They are therefore removed from the adult thorax length distribution and reflect the point at which compensation in size against mortality ceases to be effective.

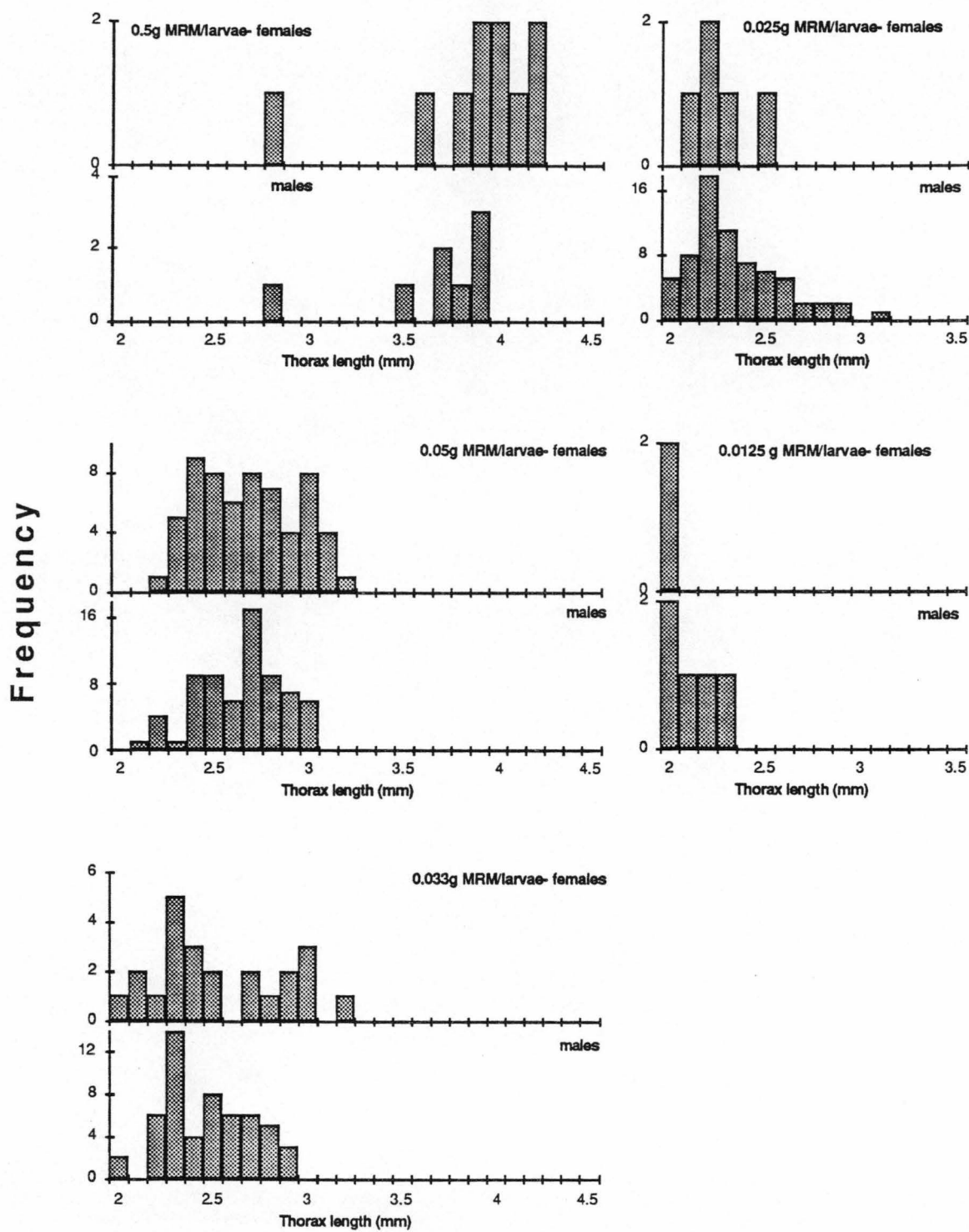


Figure 4.4 (a). Length frequency of adults (by sex) reared under different larval densities at 20°C.

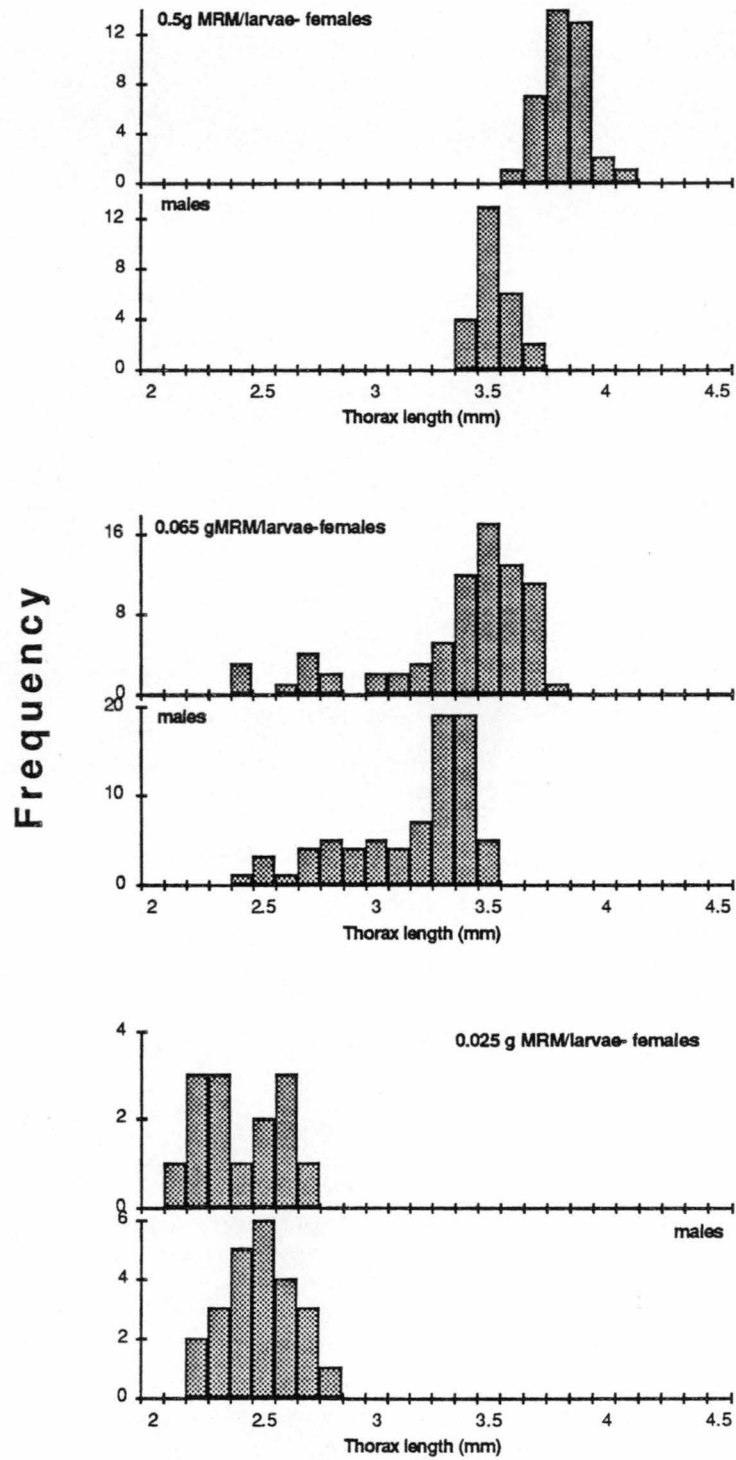


Figure 4.4 (b). Length frequency of adults (by sex) reared under different larval densities at 25°C.

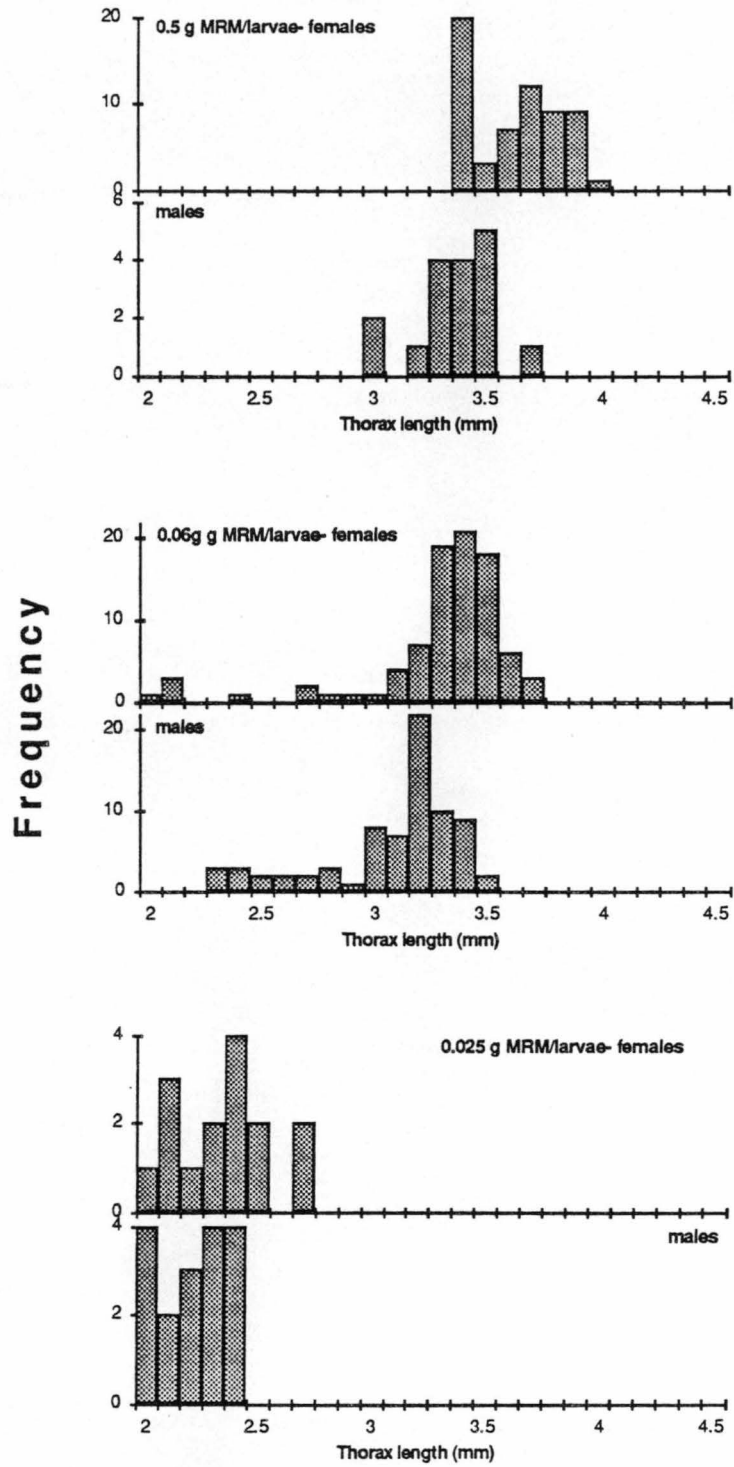


Figure 4.4 (c). Length frequency of adults (by sex) reared under different larval densities at 30°C.

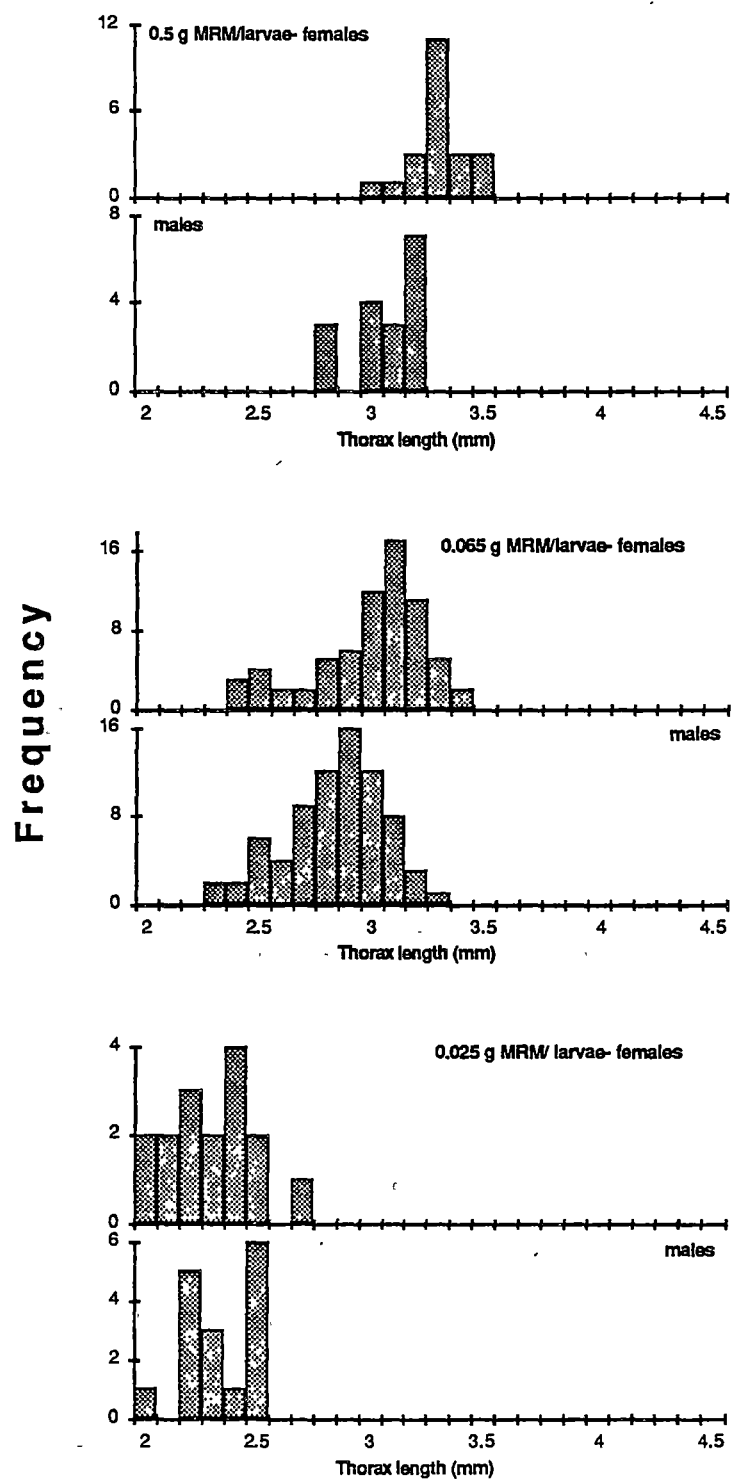


Figure 4.4 (d). Length frequency of adults (by sex) reared under different larval densities at 35°C.

Temperature (°C)	Density (larvae/g)	Thorax length (mm)			
		female	male	female	male
		mean	±SD	mean	±SD
20	2.0	3.85	0.41	3.65	0.37
	20.0	2.68	0.26	2.64	0.26
	30.0	2.54	0.34	2.47	0.23
	40.0	2.26	0.15	2.31	0.35
	80.0	2.00	-	2.12	0.13
25	2.0	3.83	0.10	3.52	0.08
	15.0	3.37	0.34	3.17	0.29
	40.0	2.39	0.19	2.48	0.16
30	2.0	3.73	0.15	3.37	0.18
	15.0	3.29	0.34	3.08	0.31
	40.0	2.34	0.21	2.21	0.15
35	2.0	3.31	0.12	3.07	0.15
	15.0	3.00	0.25	2.84	0.22
	40.0	2.29	0.20	2.33	0.16

Table 4.3. Means and standard deviations of thorax length by sex, larval density and temperature.

4.2.2 ARTIFICIAL MYIASIS EXPERIMENTS

The results of this series of experiments is given in Table 4.4 for infestation level, preadult mortality, sex ratio of emerging flies and mean male and female thorax length. In Figure 4.5 the relationship of infestation level and the final wound size is given.

Number of larvae	Number of adults	Preadult mortality	mean thorax length (mm)	
			female	male
100	89	0.11	3.68	3.41
500	450	0.10	3.65	3.38
800	761	0.05	3.59	3.33
1000	920	0.08	3.71	3.40
1500	1305	0.13	3.62	3.36
2000	1960	0.02	3.71	3.41
2500	2325	0.07	3.48	3.31
3000	2580	0.14	3.64	3.36
6000	5460	0.09	3.65	3.34

Table 4.4. Preadult mortality and mean adult size against infestation level.

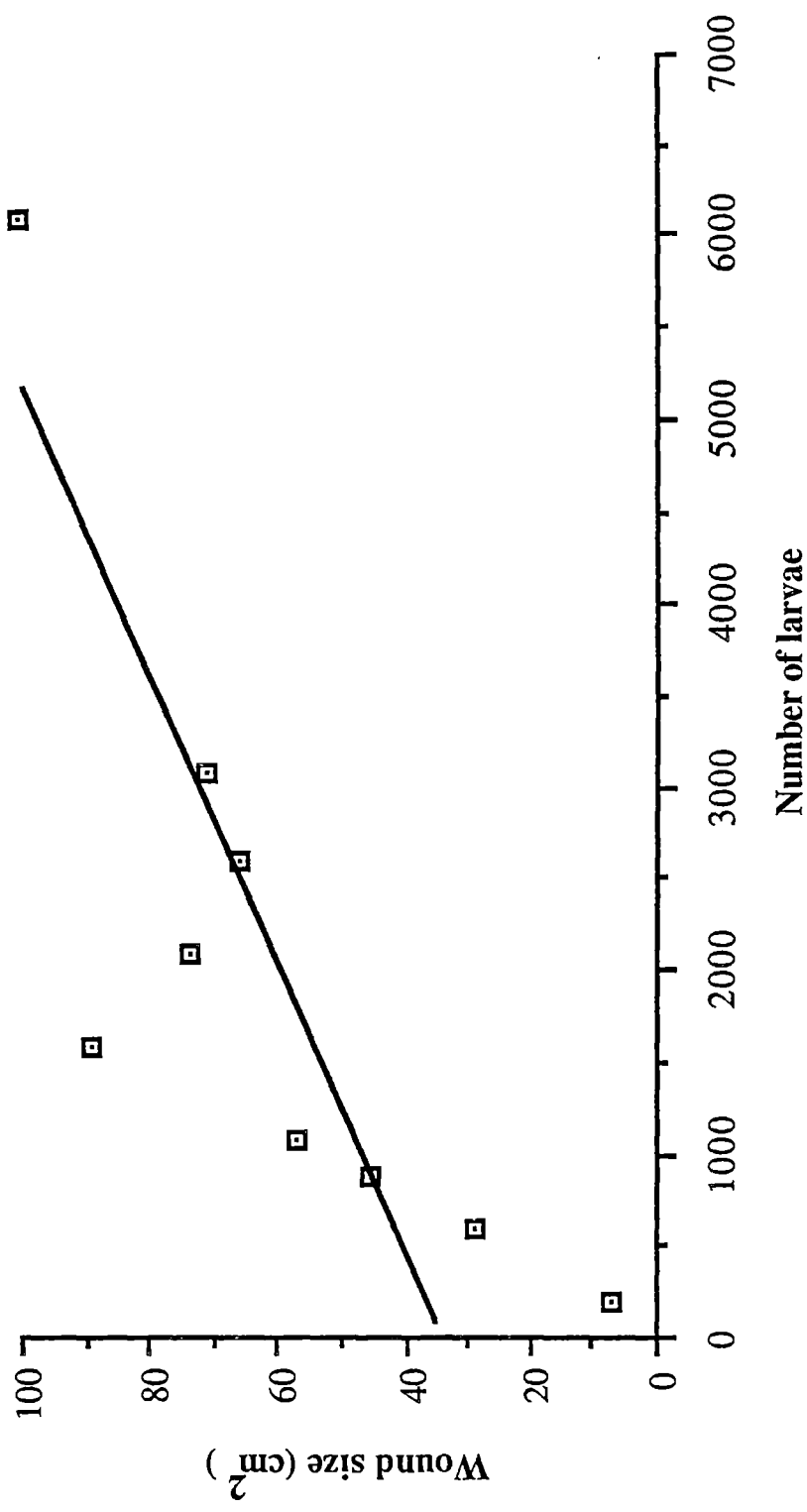


Figure 4.5. Relationship between larval density and the resultant wound size in induced myiasis. Linear regression fitted to this data.

With regard to the low preadult mortalities seen in this experiment it would seem that the method for inducing an artificial myiasis is successful. In the range of infestation levels used, no apparent change in adult fly size occurred. This would indicate that no shortage of food from the wound occurred. There is also no trend for a change in preadult mortality with increased larval numbers. Regression of the data shown in Figure 4:5 yields

$$W = 32.7139 + 0.0127 N_l$$

$$r_{(2),7} = 0.783, \text{ SE} = 19.4050, (0.02 > P > 0.01)$$

where W is the wound size (cm^2) and N_l is the initial number of larvae.

As the infestation level was raised so the final wound size increased. As the original wound size was the same in all cases, the larvae show an ability to create new areas for feeding once established on the host. It would appear that the wound size is proportional to the number of larvae established, rather than the number of larvae being limited to a myiasis prone area. This in turn points to a self regulating mechanism by which larvae gain nutrition. As the number of larvae increases the amount of wound area required to feed them increases, and new areas are occupied.

The experimental series was halted at the level of 6000 larvae per sheep due to the stress inflicted on the animal. For reasons mentioned in the Discussion it seemed pointless to go to higher infestation levels and risk the death of the host.

4.3 DISCUSSION

4.3.1 ARTIFICIAL CARRION EXPERIMENTS

The preadult mortality rates measured in the experiments reported here are in general dramatically lower than those reported for field experiments. Anon (1930) recognised that there was a high mortality for *Lucilia* spp. larvae in carrion. Waterhouse (1947) estimated that the preadult mortality of *L. cuprina* larvae in carrion was approximately 98%. A large component of this mortality was due to predation of both feeding larvae and wandering larvae. The role of parasitoids in increasing preadult mortality was also recognised by Waterhouse (1947) and Fuller (1934). More recently, Putman (1977) calculated that the preadult mortality of *C. vicina* was 80%, this was mainly due to overcompetition.

Salt (1932) found that in laboratory cultures of *L. sericata* an increase in larval density caused an increase in preadult mortality and a decrease in adult size. These observations are supported by the work described here. The difference in preadult mortality of male and female larvae which led to the significant relationships between larval density, temperature and sex ratio seen in equations [19] and [20] has not been noted in the literature. However, Sullivan and Sokal (1963) found that changes in larval density of *Musca domestica* had no effect on the sex ratio.

Williams and Richardson (1984) found that larvae of *L. cuprina* would grow in temperatures of 15 to 40°C. Development rates were linear over this range, as they were in the more limited range reported here. Sullivan and Sokal (1963) found that the mean and variance of development time in the preadult stages of *M. domestica* increased with density. The trend for increased development time is seen in these experiments, however as replicates of each treatment were not kept due to the logistics of the experiments, the measurement of variance around development rate cannot be calculated.

Ulyett (1950) noted that with overcrowding the development time of *Lucilia* spp. was increased, as was mortality. He also found that the mortality of pupae was independent of crowding. As the number of pupae formed was not measured over the whole range of densities tried in the experiments recorded here his observations cannot be confirmed.

Hughes *et al.* (1972) found that the relationship of the length of the pharate stage of *M. vetustissima* to ambient temperature was linear. In the experiments reported here the development periods are essentially linear over 20-35°C, whilst no development is seen at 40°C as pupae failed to form in these cultures.

For adult females in the pharate stage, Sands and Hughes (1977) found that the larger flies of *M. vetustissima* had a more rapid reproductive development than smaller ones. With regard to ovarian development rates for *L. cuprina*, Woodburn *et al.* (1978) found that they were linear within the range of 10-45°C. Both these observations are confirmed here for *L. cuprina*.

The relationship between adult female body size and clutch size is well known for *L. cuprina*. Webber (1955) calculated an allometric relationship of thorax length (mm) to the total number of ovarioles which is given below.

$$N_{Ov} = 1.81 Tl_f^{2.39}$$

The relationship describes the same trend as that reported here. The differences in the regression constants are difficult to relate to tangible measures and may simply be due to parallax errors, that is, his measurements were made laterally while those used here were measured on the dorsal surface. Kitching (1981) reports an allometric relationship between headwidth and clutch size.

Ulliyett (1950) found that the clutch size of female *Lucilia* spp. decreased with increased competition, and this observation is confirmed here. Williams and Richardson (1983) looked at the variation in female gonad:somatic tissue ratios of *L. cuprina*. adults from the range of sizes possible. They found that although smaller flies have a smaller clutch size, they have a higher commitment in relative body weight to reproduction.

The relationship of adult size to survival for *L. cuprina* has not been examined before. In relation to temperature, Salt (1932) found that the mean longevity of *L. sericata* was 41 days for males and 55.6 days for females in cultures maintained at 18-28°C. This general relationship of male survival being less than that for females is seen here. Kitching (1981) reported a median laboratory longevity of 400 D° for *L. cuprina*. Effects of size differences have been reported from ~~from~~ field experiments for *M. vetustissima*. Sands and Hughes (1977) found that larger flies were represented more frequently in the older age classes of trapped *M. vetustissima*. They concluded that survival was proportional to size, as in the relationship recorded here.

4.3.2 ARTIFICIAL MYIASIS EXPERIMENTS

Developmental rates of larvae in myiasis are not governed by environmental temperatures but rather by the temperature in the fleece of the host. Skin temperatures may range from 34-42°C (Vogt and Woodburn, 1979). Vogt and Woodburn (1979) also note that the presence of larvae on the skin will ensure the supply of the protein rich serous exudate upon which the larvae feed. These factors enhance myiasis as a stable larval habitat.

Vogt and Woodburn (1979) note the need to break the skin for a successful induction of artificial myiasis. Even after this preparation they suggest that conditions in

artificial myiasis are not initially suitable for larval growth as compared to natural myiasis where a predisposing factor is involved. This condition is supported by the larval survival rates reported by Foster *et al.* (1975). In that study a maximum survival rate of 50% was calculated. In the present study the survival rates recorded are significantly higher with a maximum of 95%.

The levels of infestation used here are within the range of other studies. For example, Smith *et al.* (1981) used infestation levels of 4500-6300 eggs per sheep (the hatching rate is unknown). Under natural conditions, Waterhouse (1947) calculated that the average size of a strike was 1,220 larvae per sheep (with a range from 37 to 9,704).

Where myiasis is fatal the host can become a super source of adult flies. Cragg (1955) suggested that this occurred for *L. sericata* in Britain, where the larvae present before death were favoured after the death of the host by both temperature and the lack of competition. Competition is reduced in comparison to carrion as the original larvae are more advanced than the larvae derived from flies visiting the carcass are likely to be. They would thus finish their feeding before the other larvae were large enough to interfere with their development. This condition has also been noted for *L. cuprina* in Australia (Kitching, 1981).

4.3.3 GENERAL CONSIDERATIONS

In the experiments discussed in this chapter, thorax length has been correlated to density of larvae on limited substrates. In each instance the distribution of thorax length around the mean has been normal. Thorax lengths of flies from artificial myiasis also have a normal distribution.

In contrast to the outcome from artificial carrion, the size of flies from artificial

myiasis were seen to be independent of density. These densities reflected the natural levels of myiasis recorded in other studies. Where strike has a fatal outcome for the host the resultant adults of the original larvae are likely to be near optimum size. Given that overcompetition occurs for *L. cuprina* in carrion then the adults are likely to be below the optimum size. These tendencies support the idea that the original larval habitat will be reflected by adult size.

A similar approach has been employed by Hughes and Nicholas (1974), who recognised cohorts of *M. venustissima* by the distribution of the head capsule width. As reproductive development rates vary with size, and development stages can be recognised, a further level of separation for cohorts of *L. cuprina* may be possible. That is, a cohort should be composed of flies of a similar size range as they are derived from the same larval density. The reproductive development rates for this size are more or less the same so their ages (measured by reproductive maturity) should also be distributed more or less normally. As a field sample of flies from trapping may be composed of several cohorts, separation on these two parameters may be possible. This idea is tested in the next Chapter.

Roff (1981) demonstrated that a wide variations in life history parameters, such as survival and fecundity as functions of size, have small effects on the the optimum body size. That is, an optimum size does not exist but rather occurs within a wide range of sizes. Optimal size for *L. cuprina* has important implications to the perception of its ability to persist. It is traditionally thought that flies from carrion are few and small. Small flies are seen to be 'less fit' and therefore less able to contribute to the maintenance of a population. The results of this Chapter will be applied to this question in Chapter 6.

4.4 CONCLUSIONS

Note: all conclusions relate to *Lucilia cuprina*.

- (i). Adult size and mortality are related to larval density in carrion.
- (ii). Adult male size is less than that of females reared at the same larval densities.
- (iii). A high correlation exists between female size and clutch size.
- (iv). Pupae will not form at temperatures equal to or exceeding 40°C.
- (v). Development rates for larvae, pupae (pharate), teneral adults and adult mortality are linear over the range 20-35°C.
- (vi). Development rates are generally increased with decreased adult size.
- (vii). Adult mortality is increased with decreased adult size.
- (viii). The relative proportion of males becomes larger with decreased adult size.
- (ix). Density has no effect on mortality in artificially induced myiasis in the range measured.
- (x). Adult size is not related to density in artificially induced myiasis.
- (xi). Wound size and larval density are correlated.

CHAPTER 5.

DETECTING THE EFFECTS OF COMPETITION IN FIELD POPULATIONS OF SHEEP BLOWFLIES.

5.0 INTRODUCTION

It has been demonstrated in the previous Chapter that the degree of competition has a direct effect on adult size in simulated carrion but not in myiasis. Cohorts reared at fixed densities are also seen to have defined distributions around the resultant mean adult sizes. These results suggest that in the field cohorts arising from carrion would have mean sizes distributed over a wide range of possible sizes whilst those from myiasis would be distributed around the optimal size.

Measurement of the size composition of a field sample of flies may then yield some indication of the number attributable to either larval habitat. The proportion of the number of flies below the optimal size range to the number in the optimal size range would be an estimate of the lower bound of the proportion emerging from carrion. It is an estimate of the lower bound because it is possible for flies from carrion to be at optimal sizes; this however is unlikely due to the common occurrence of competition in carrion.

A field sample is likely to include flies from several larval cohorts and it is therefore possible that the size ranges will overlap. However, given that carrion is distributed randomly in time, and that myiasis is also more or less randomly distributed, then the cohorts developing from them will also be produced in a random temporal succession. A field sample will then be composed of flies from cohorts with different size distributions and age distributions. If it were possible to separate cohorts by plotting the frequency of flies from a sample into size and age classes then it would be a powerful tool

for measuring population dynamic parameters directly in the field.

Spatial localisation of emergence sites for cohorts from myiasis is likely, due to the interaction of sheep and wandering larvae behaviour. Sheep have predictable movements and camp at favoured sites at night (Arnold and Dudzinski, 1978). Wandering larvae leave the host at night and should therefore accumulate at camp sites (Smith *et al.*, 1981). The localisation of emergence site for flies from carrion is ensured by the immobility of the larval resource. Since cohorts will have localised emergence sites then the dispersal of adult flies with age should be detectable by spatial autocorrelation.

In Chapter 3 an experiment using sheep carcasses to determine the species mix emerging from carrion was described. Additional results of these trials, concerning the size distribution of flies emerging, will be presented in this Chapter and compared to the field data.

This Chapter sets out to examine the feasibility of the cohort separation technique and to apply it to field samples. Adult sizes and the proportions attributable to different larval habitats are also examined. Spatial autocorrelation will be used to identify patterns in the distribution of particular age groups over the trapping grid and thus give an indication of variation in dispersal patterns with age.

Whilst ageing flies by examining their ovaries, clear signs of the failure by gravid flies to oviposit were seen in the form of resorbing eggs. The frequency of occurrence of this state was monitored to give a general picture of reproductive success in the field and the effects of size on the success rate.

5.1 METHODS

5.1.1 MEASURING AGE AND SIZE DISTRIBUTIONS

Flies used in this analysis were those collected in the regular lattice sampling at "Chiswick", Ross, described in Section 3.1.2.1. Both *L. cuprina* and *L. sericata* were used, but measurements were only made on female flies. This was done for two reasons. The first was to remove the confusion in the length distributions if male and female sizes were pooled. It has been demonstrated in the previous Chapter that males are smaller than females reared under the same conditions, thus males and females from the same cohort would have different size distributions. The second reason involves confusion in temporal separation. Males emerge sooner than females and are also difficult to age. The easiest ageing technique is based on the development of the female reproductive system and so is obviously not suitable for males. As the number of males in samples is small in comparison to the number of females there is no significant loss of data.

Size was measured as thorax length as described in Section 4.1.2.1. Ageing was carried out using the technique described by Vogt *et al.* (1974). For this technique the ovaries were dissected from the flies and prepared as in Section 4.1.2.1. They were then examined under a compound microscope. Stages were allocated using the definitions of Vogt *et al.* (1974) and these are summarised below.

- Stage 0: Ovaries small, rounded bodies, white and compact. Developing follicles are rounded. The ovary is tightly enveloped by the tracheal system.
- Stage I: Eggs becoming translucent and follicle becoming oval in shape. No yolk visible.
- Stage II: Eggs oval in shape and yolk occupying up to 35 % of the eggs near proximal end.
- Stage III: Ovary is larger and looser in appearance and individual eggs are clearly visible. They are elongated and the yolk occupies 35-75% of

the follicle. Secondary follicle at Stage I.

Stage IV: Eggs are nearly full size with yolk occupying 75-100% of the follicle.

The integument of the egg is fragile and often breaks on dissection.

Stage V: Eggs fully mature with tough chorion. Egg is slightly curved and has a distinct hatching pleat down one side.

This schema describes development within an egg laying cycle of the adult fly. Stage 0 only occurs in the first cycle with subsequent cycles starting at Stage I (following Stage V). The number of preceding cycles that have occurred can be determined from the size and density of the follicular relic found at the base of the ovariole. This technique is reliable up to the fourth gonadotrophic cycle (Vogt, *et al.*, 1974). In the following text the convention for annotating cycle and stage will be to refer to cycle (numeric). stage (Roman); for example stage 3.IV for a female in the third gonadotrophic cycle and fourth ovarian stage of development.

Failure of the female to find suitable oviposition sites at Stage V results in the resorption of the egg and a developmental delay in the normal progression to Stage I of the next cycle. This state is easily identified in the follicles (see Plate 5.1). The frequency of occurrence of resorption was noted at the time of ovary staging.

The age and size class of each individual female fly was scored in a two dimensional matrix. This resulted in a three dimensional age-size frequency distribution (x and y being size and age respectively and z being frequency). These distributions were collated by species, trapping day and trap site within the grid.

5.1.2 CARRION EXPERIMENTS

The size distributions of the *L. cuprina* and *L. sericata* emerging from the controlled carrion experiments described in Section 3.1.3 were measured by the technique

described in Section 4.1.2.1.



Plate 5.1. Resorbing eggs in a stage I female of *Lucilia cuprina*.

5.2 RESULTS

5.2.1 THE RELATIVE IMPORTANCE OF LARVAL HABITATS

In Section 4.2.1 it was shown that larvae of *L. cuprina* reared in artificial carrion gave rise to adults covering all sizes in the species size range, dependent on larval density. In comparison, the results presented in Section 4.2.2 demonstrated that *L. cuprina* reared from myiasis were consistently of a large size. From this data a generalised mean female size and standard deviation were calculated for *L. cuprina* emerging from myiasis. This figure was 3.65 ± 0.167 SD mm thorax length. The lower 95% confidence limit of this distribution is at the 3.3 mm thorax length size class. In the following text, flies smaller than 3.3 mm thorax length will be referred to as *high density flies* (referring to their larval habitat) and those of 3.3 mm or larger as *low density flies*.

Size frequency distributions for each trapping day and for the whole season are presented in Figure 5.1 a and b for *L. cuprina* and *L. sericata* respectively. It is apparent from Figure 5.1a that the strongest modes are around 3.3-3.5 mm thorax length, within the *low density fly* size range for *L. cuprina*. Where sample sizes are larger for *L. sericata* (excluding the 26 February and 3 March 1984 samples) the size distributions are notably more widely spread than for *L. cuprina*.

As a crude indicator of the importance of the alternative larval resources in contributing to the adult field population the number of *high density flies* of *L. cuprina*, was totalled and compared to the season's total figure. It is possible for flies from carrion to be of sizes ranging up to the maximum size, and unlikely for flies from myiasis to be smaller than 3.3 mm. Because of this the indicator should be an underestimate of the number of flies attributable to adults reared from carrion. For the season's total the proportion of *high density flies* was 18%.

Figure 5.1 (a). Size frequency of *L. cuprina* from field samples by trapping day and with seasons' total.

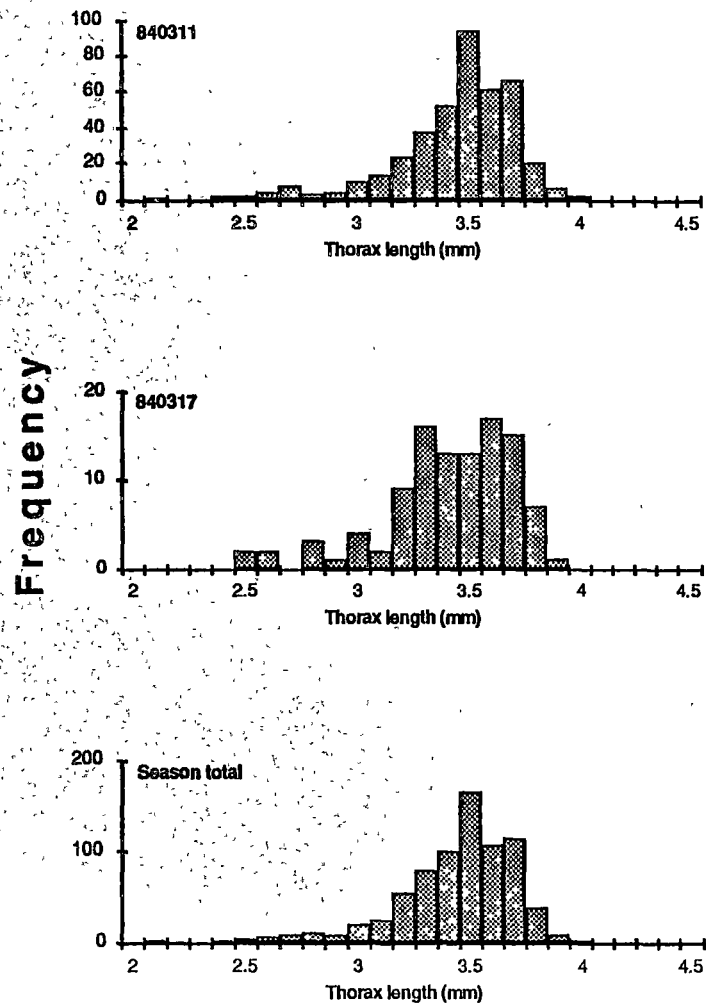
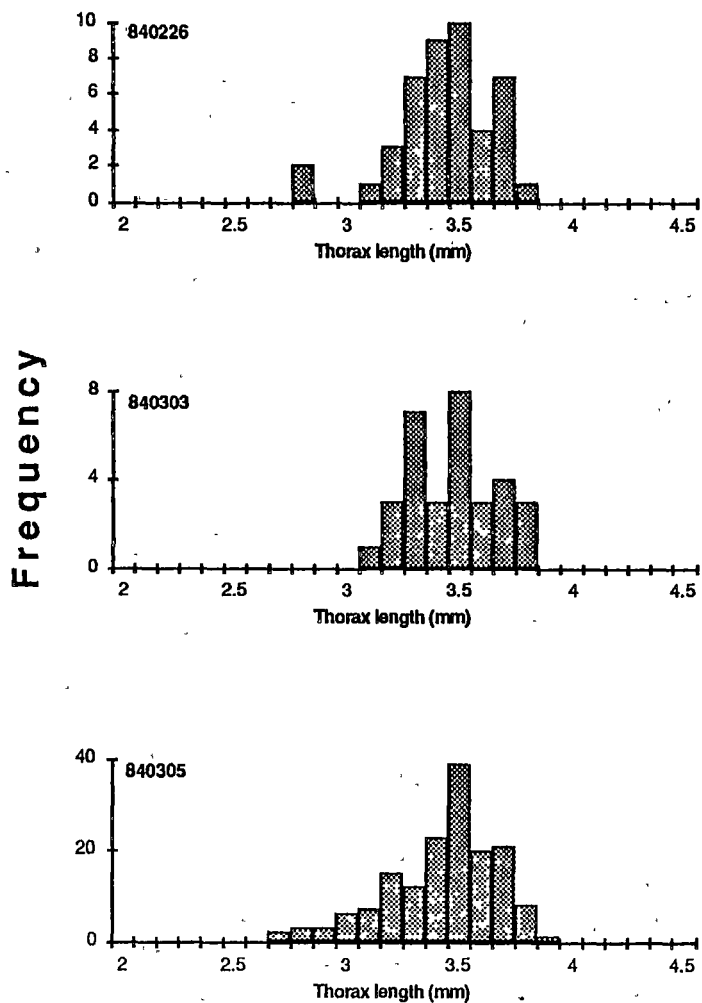


Figure 5.1 (b). Size frequency of *L. sericata* from field samples by trapping day and with seasons' total.

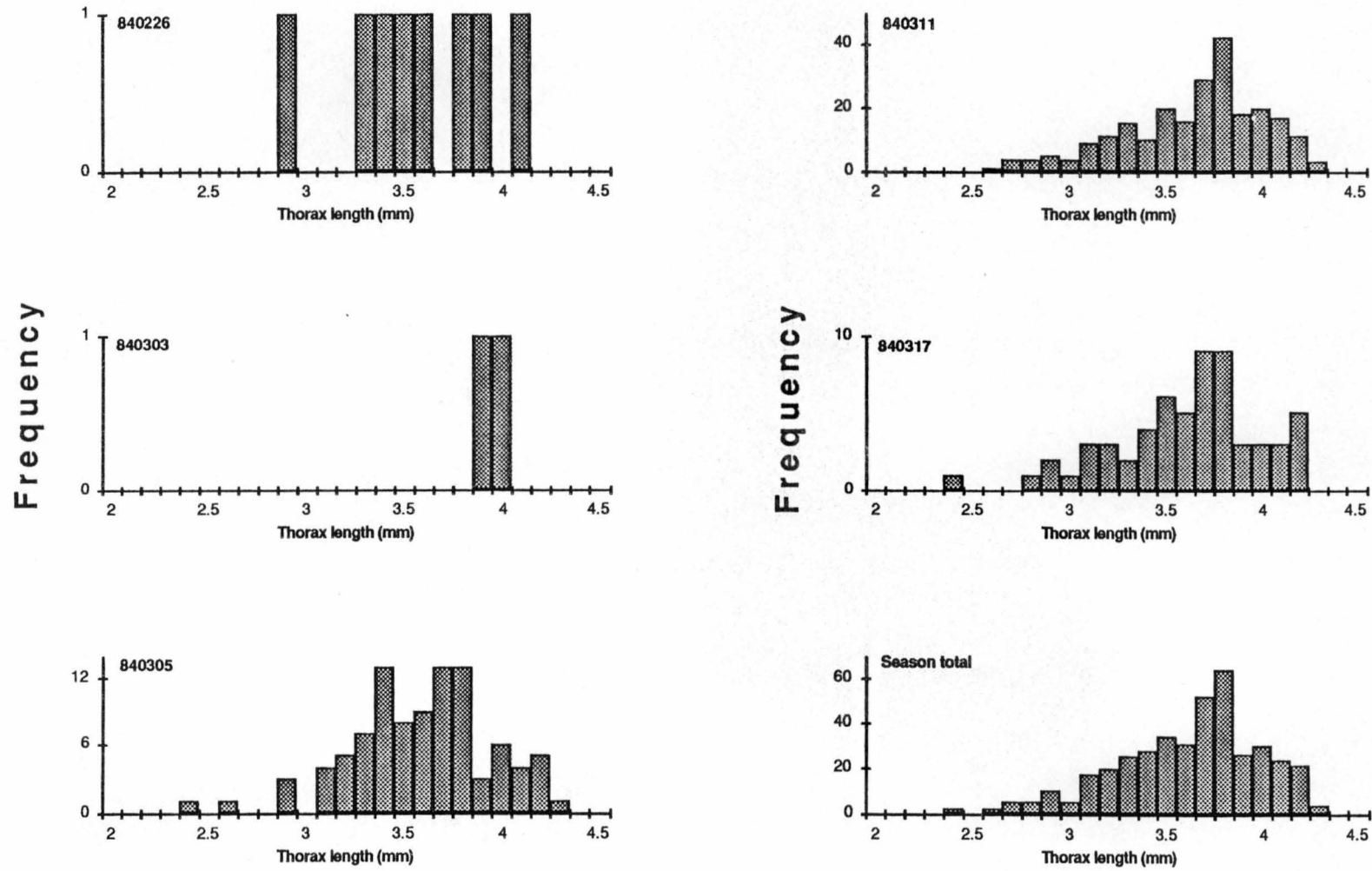
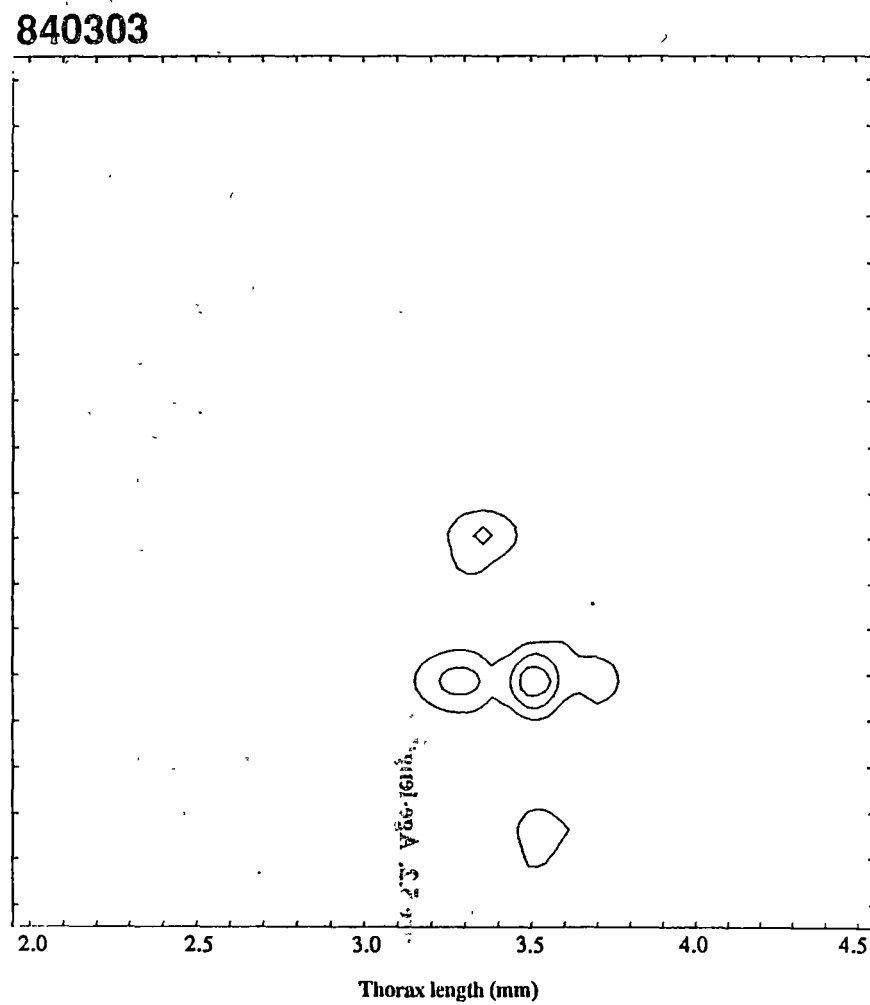
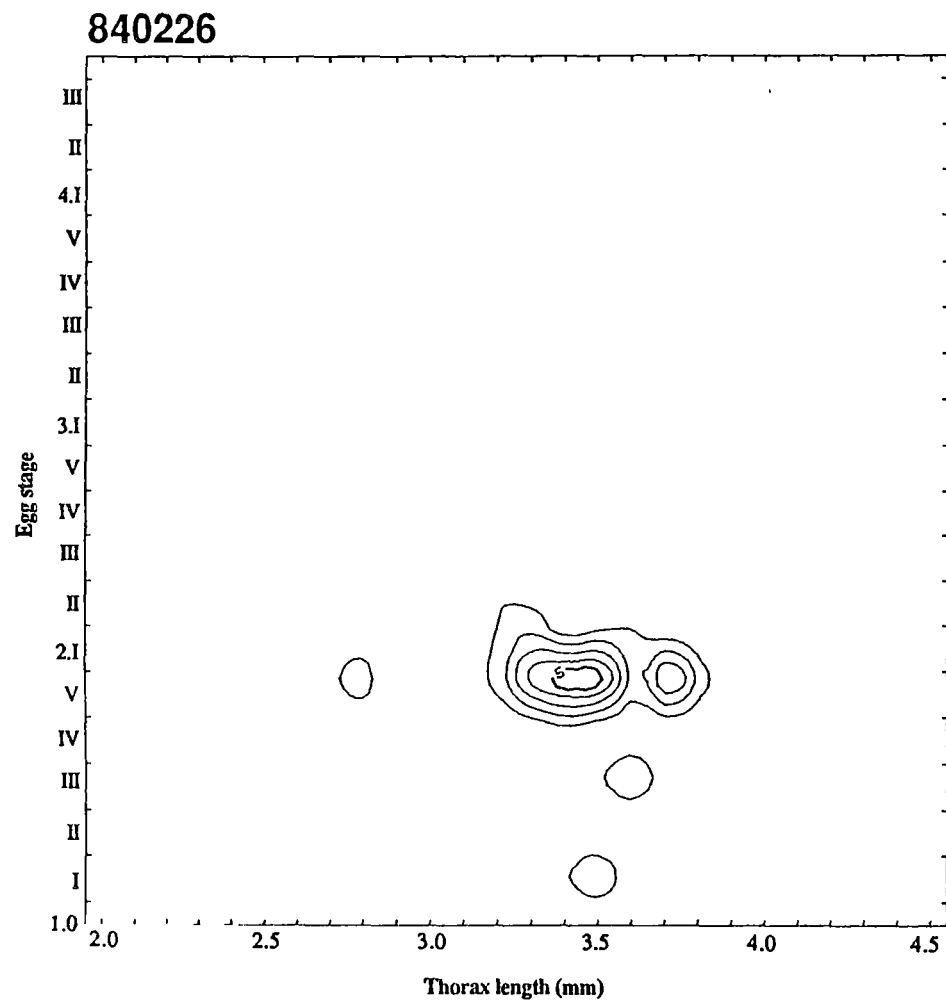
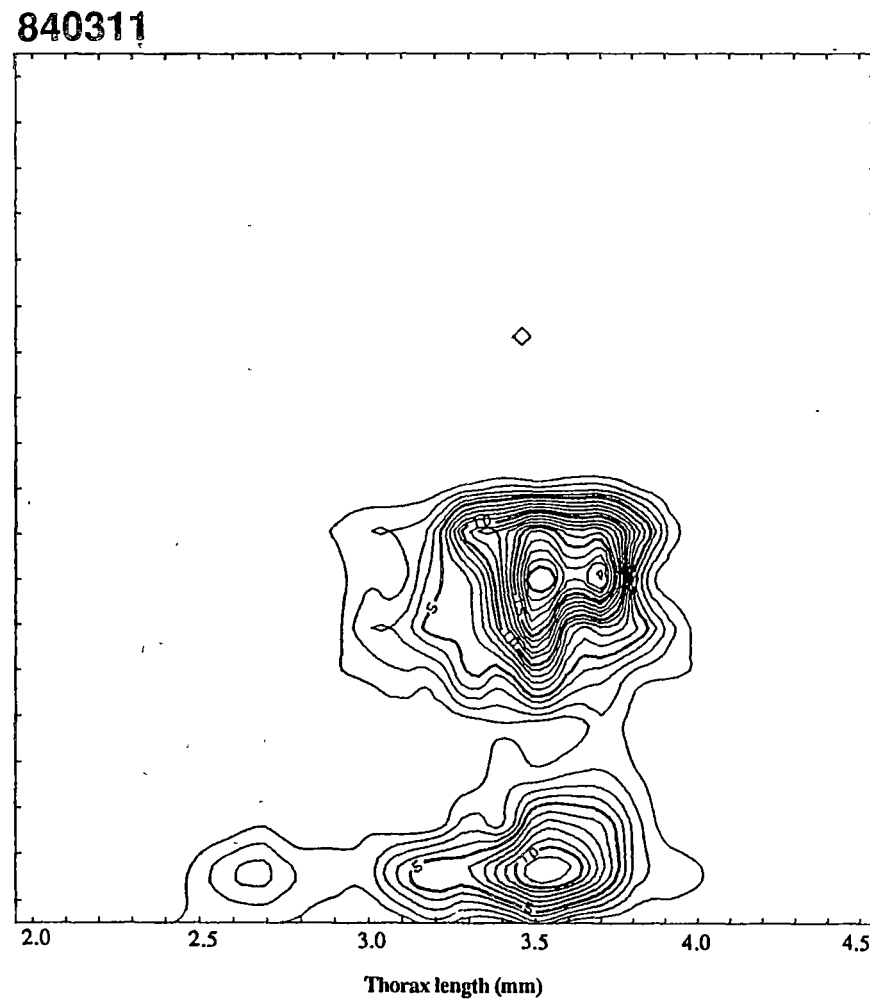
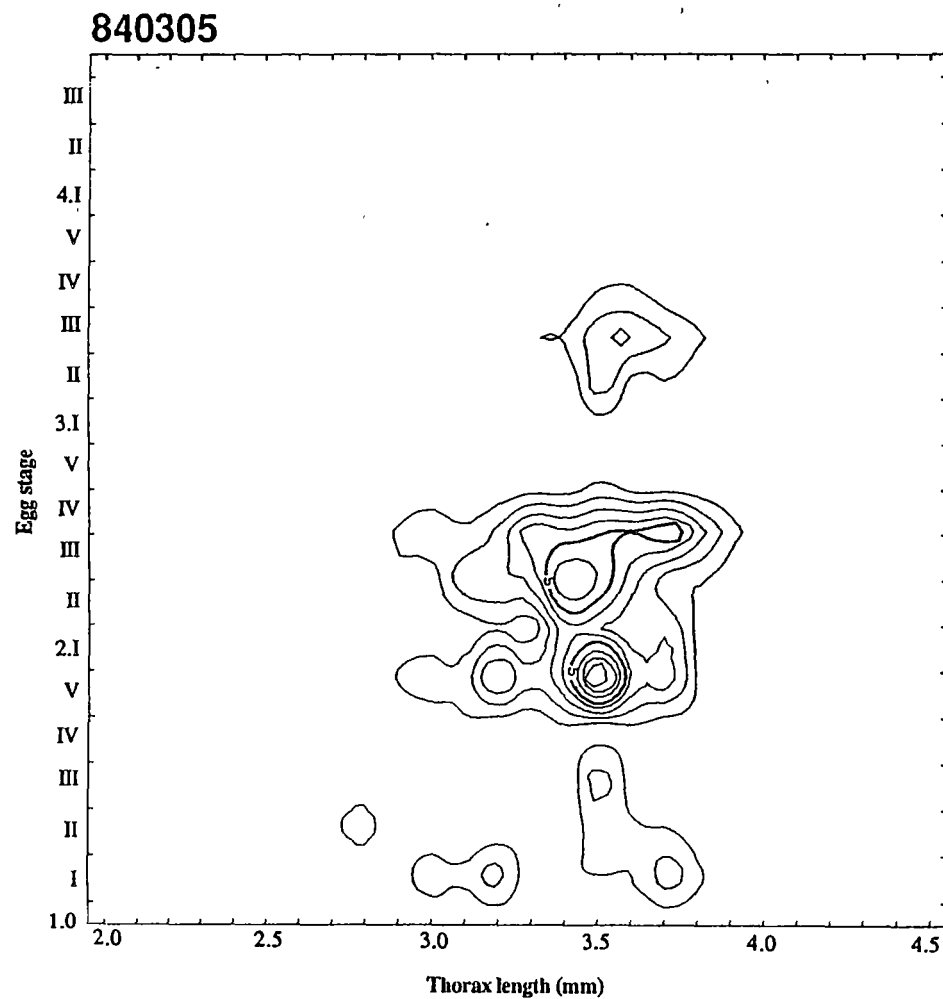


Figure 5.2. Age-length class frequency distribution of *L. cuprina* by trapping day (YYMMDD).

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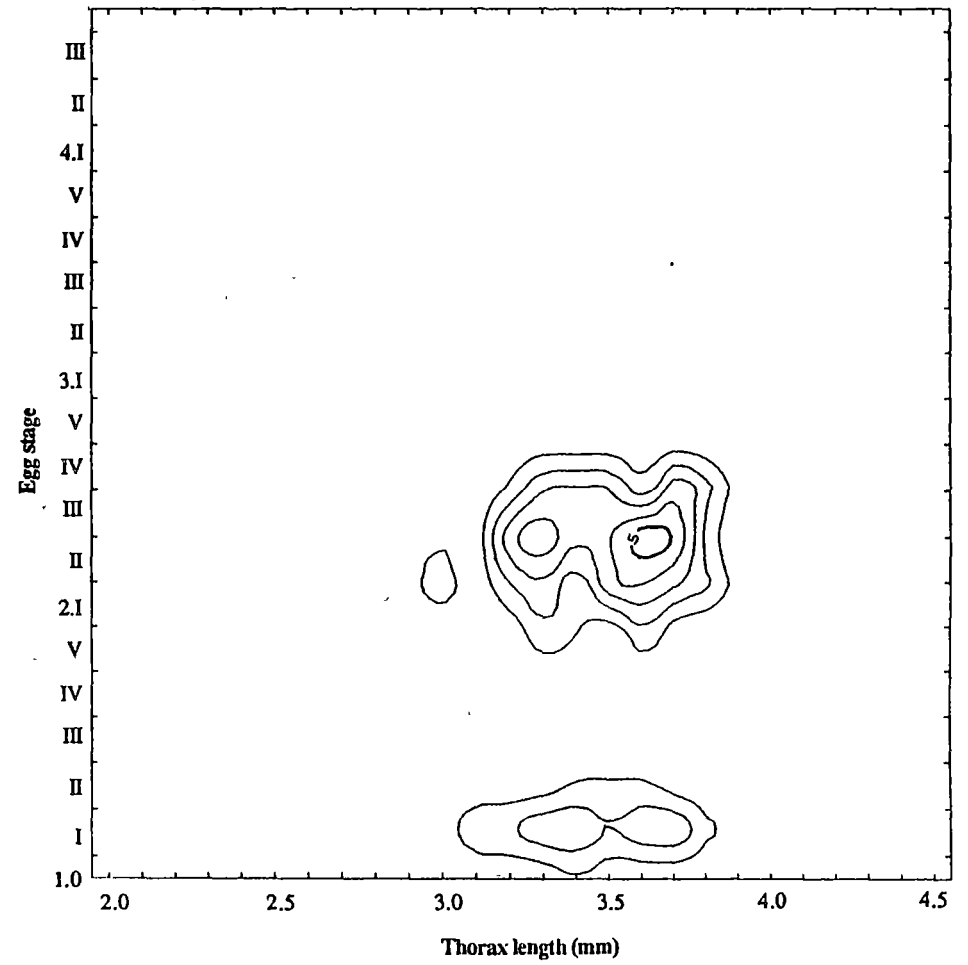
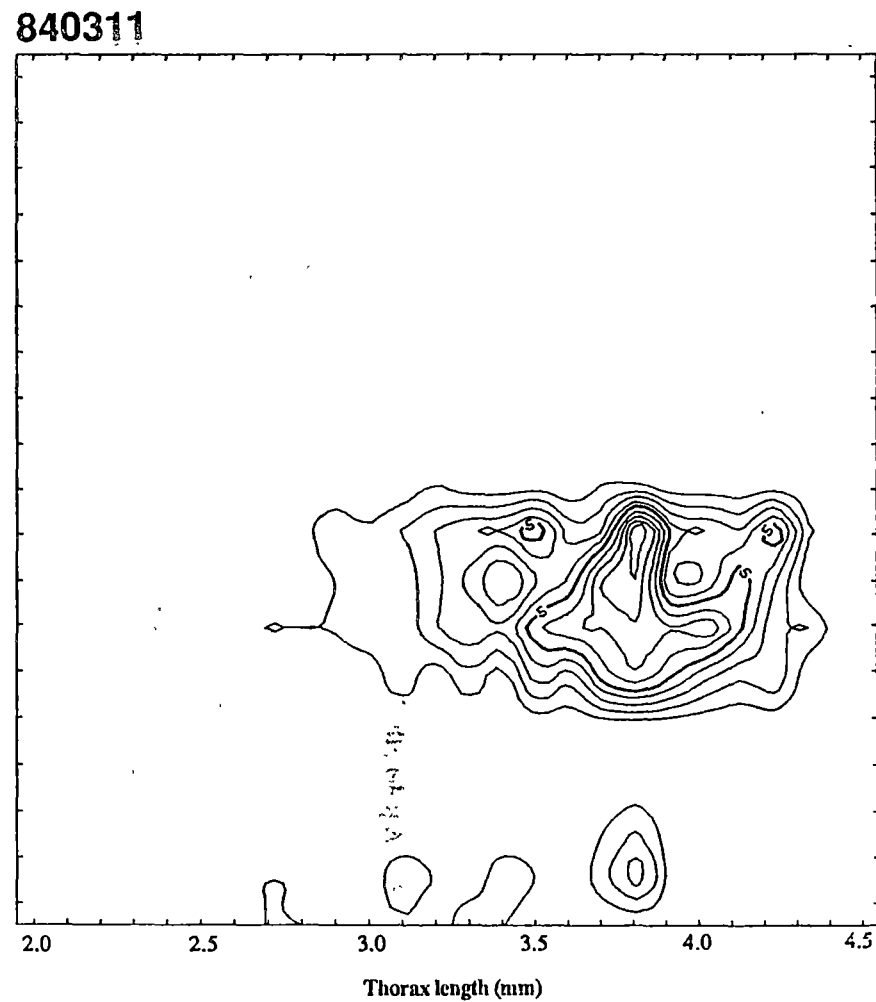
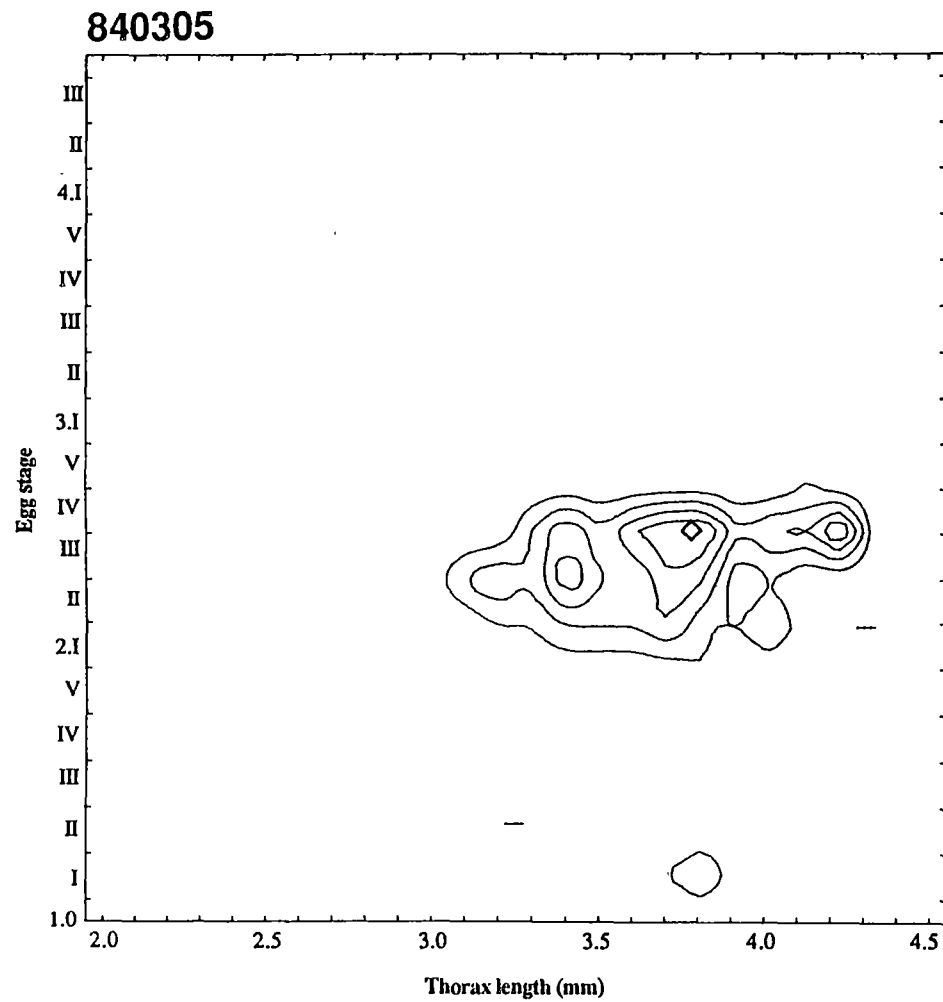
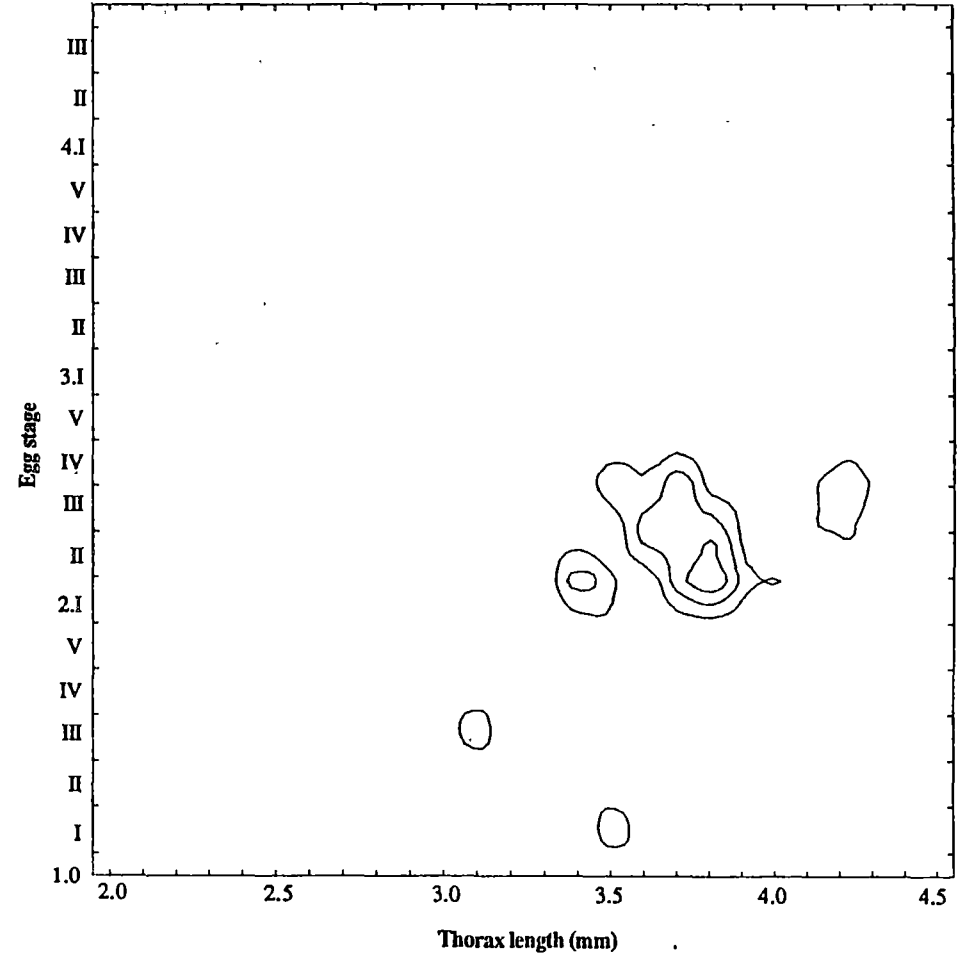


Figure 5.3. Age-length class frequency distribution of *L. sericata* by trapping day (YYMMDD).

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5.2.2 COHORT SEPARATION

Because of the clumped distribution of *L. cuprina*, sample sizes between different trap sites within the grid were highly variable. Most sites had very low sample sizes, a few (especially those associated with the carcasses described in Section 3.1.3) were high. Similarly for *L. sericata* densities were generally very low.

For these reasons there was no basis for comparison of the age-size frequency distributions between trap sites. This meant that the identification of spatial changes in cohort distribution could not be performed. The data were then pooled for each trapping day and are presented as SURFACE 2 plots in Figures 5.2 and 5.3 for *L. cuprina* and *L. sericata* respectively. The seasons total age-size distribution is given in Figure 5.4.

Statistical analysis for the separation of two dimensional distributions are extremely complex. At this time no method has been developed for the analysis of distributions composed of continuous (size) and discrete (age class) variables. Because of these problems the age-size distribution technique was assessed by visual inspection of the trapping day grid totals.

From these Figures it can be seen that some age groups are absent or under-represented. These age groups correspond to stage II,III for the first two trapping days and stage IV in all samples. These stages are less motivated by protein odours than stage I and V, and are thus less vulnerable to trapping in a bait trap, (Kitching, 1981). For these same reasons stage I and V are usually over-represented, due to their active searching for protein either for the development of eggs (in stage I) or for oviposition sites (stage V).

Because protein resources may be limited in the field, ovarian development delays can occur at stage I and V (Kitching, 1981). This results in flies accumulating in these

stages, another source of over-representation (Vogt, *et al.* 1974). Where developmental delays occur, the physiological age of flies will be greater than that indicated by the aging technique.

The action of developmental delays on cohorts would spread the age classes over a wider range. The emergence period of a cohort can also be a source of variation in age. Pupal development is governed by temperature and so where temperature is low, emergence may take place over a protracted period (Foster, *et al.* 1975). Together these factors introduce a significant amount of noise on the ovarian age axis which cannot be compensated for.

Evidence of developmental delays due to lack of oviposition sites became apparent (in the number of females resorbing eggs) during the course of this analysis and is discussed below. Because of the relatively high frequency of resorption it had to be assumed that the age distributions were significantly distorted, and so no further analysis of the age-size distribution data was performed.

The age distributions alone for each trapping day and season totals are presented in Figures 5.5 a-f and 5.6 a-f for *L. cuprina* and *L. sericata* respectively. A point of interest in these graphs is the accentuation of stage 2.V in the first trapping days for both species, and the decline in the strength of this stage as the season progressed. This phenomenon suggests that oviposition sites are limited resulting in females accumulating in this stage. Later in the season stages 2.II and 2.III become dominant. Sands and Hughes (1979) [from a study on *Musca vetustissima*] suggest that this distribution is related to either a lack of males for fertilisation or to insufficient protein sources being available to provide the females with the protein required for egg development.

Figure 5.4. Seasons' total of age-length class frequency distribution for *L. cuprina* and *L. sericata*.



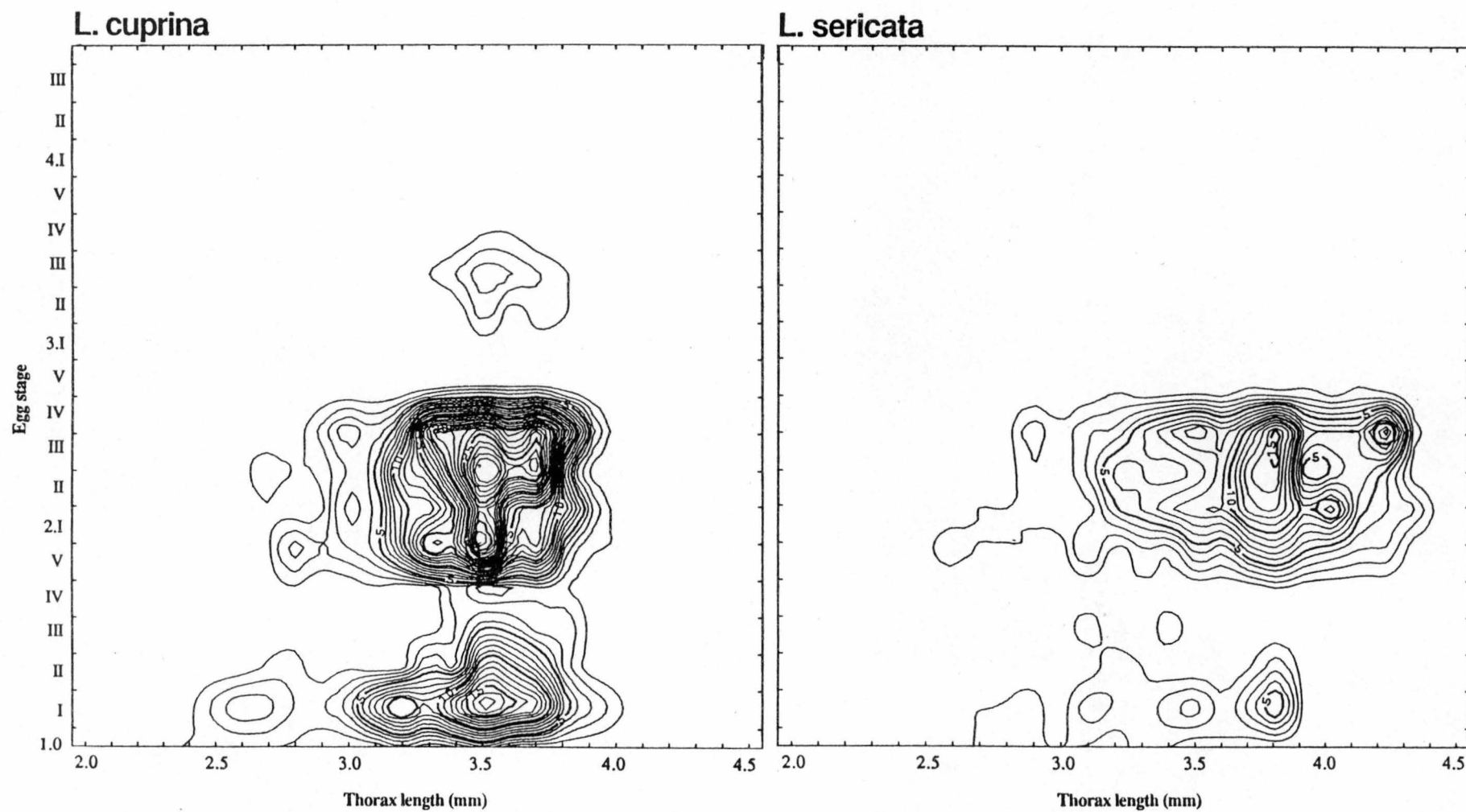
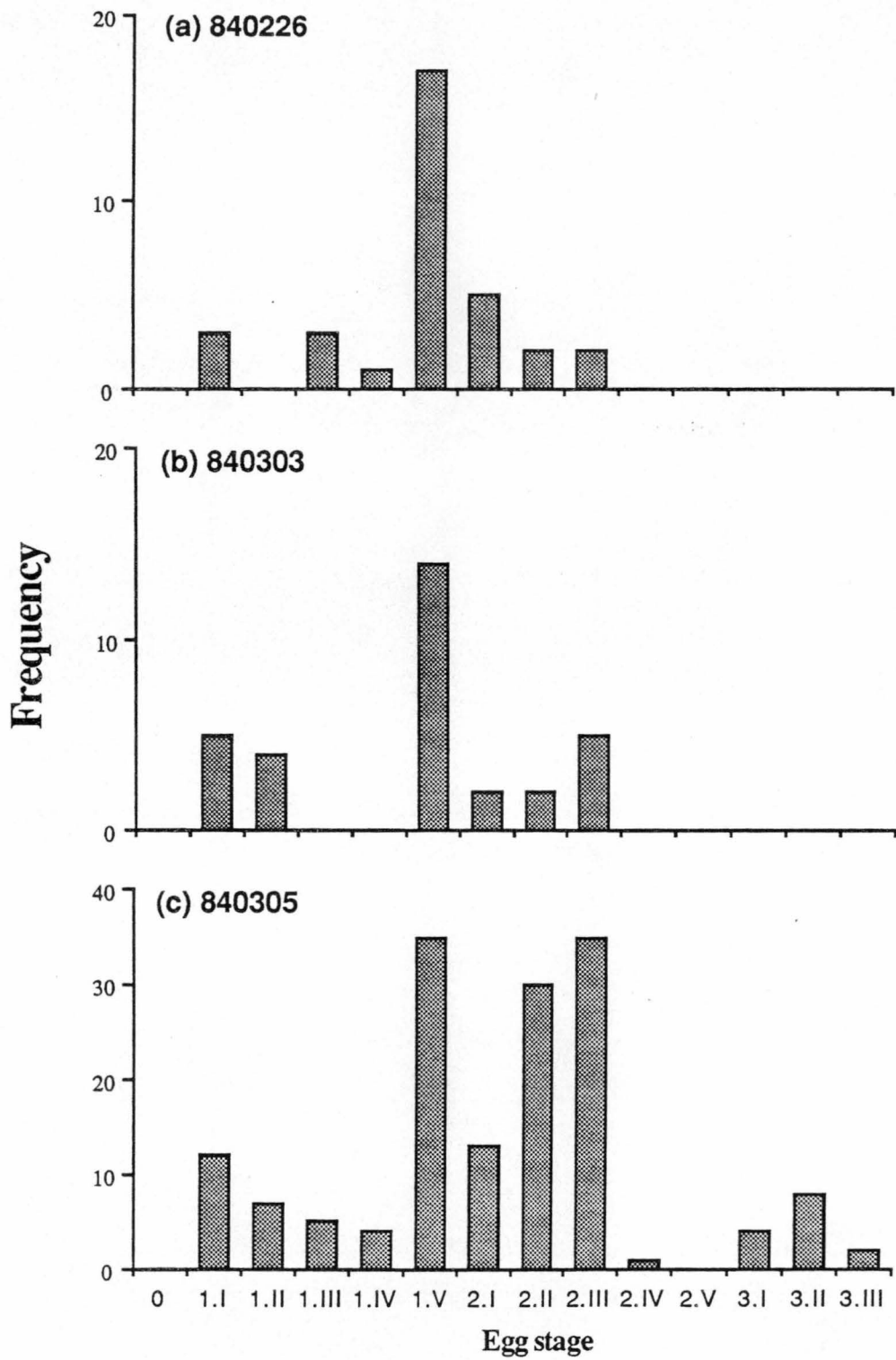


Figure 5.5. Ovarian age distribution of *L. cuprina* on each trapping day and with seasons' total.





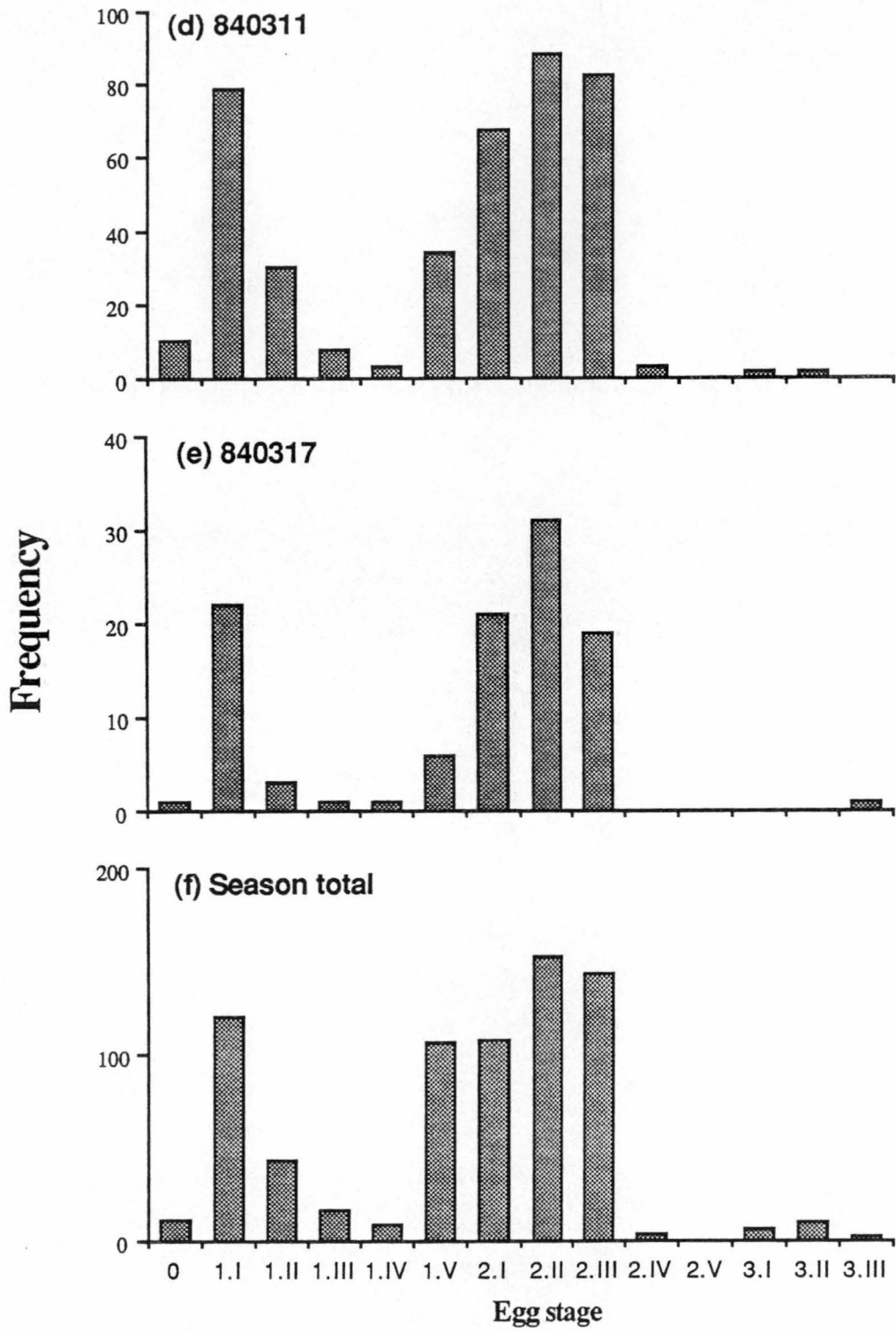
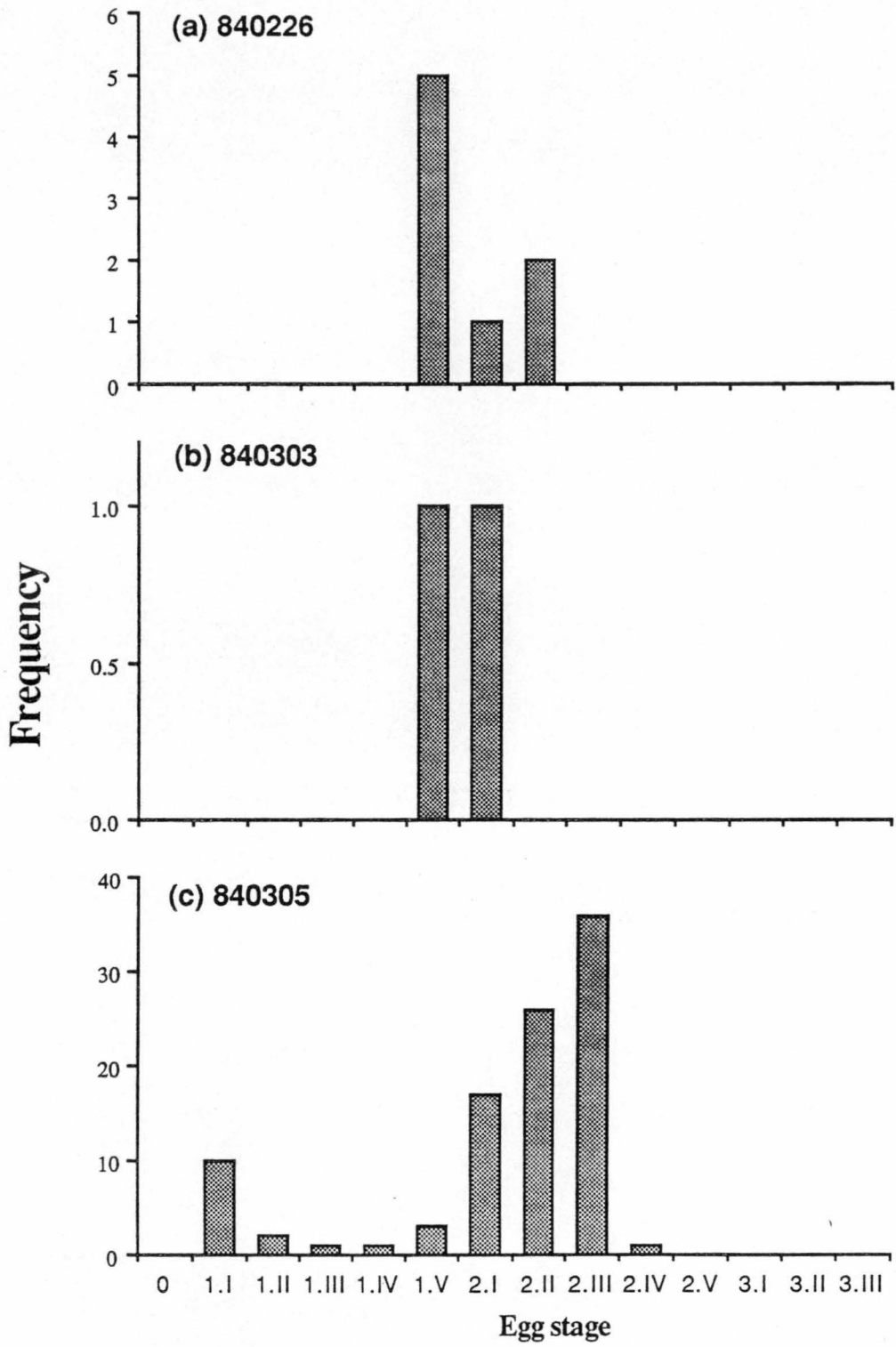
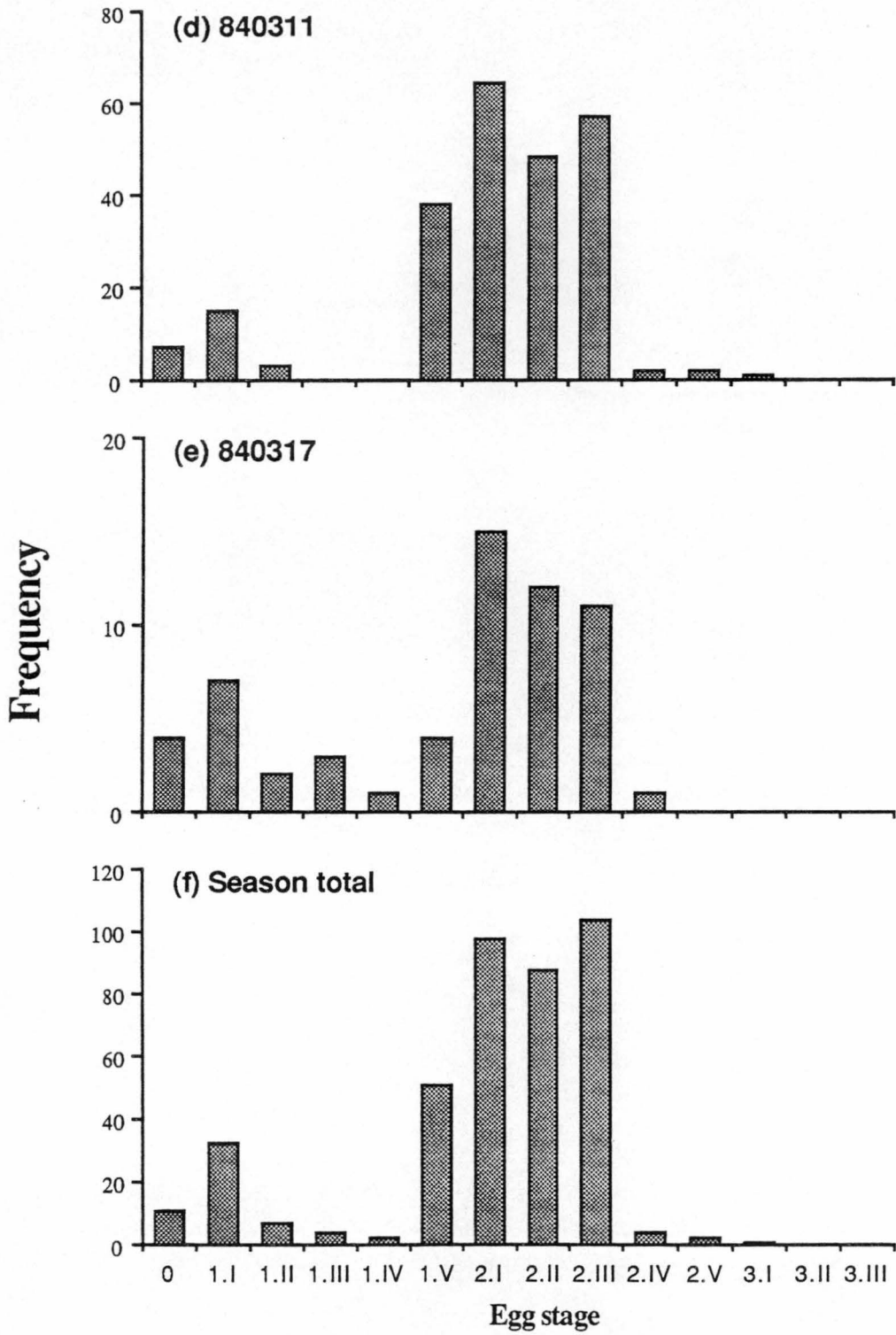


Figure 5.6. Ovarian age distribution of *L. sericata* on each trapping day and with seasons' total.





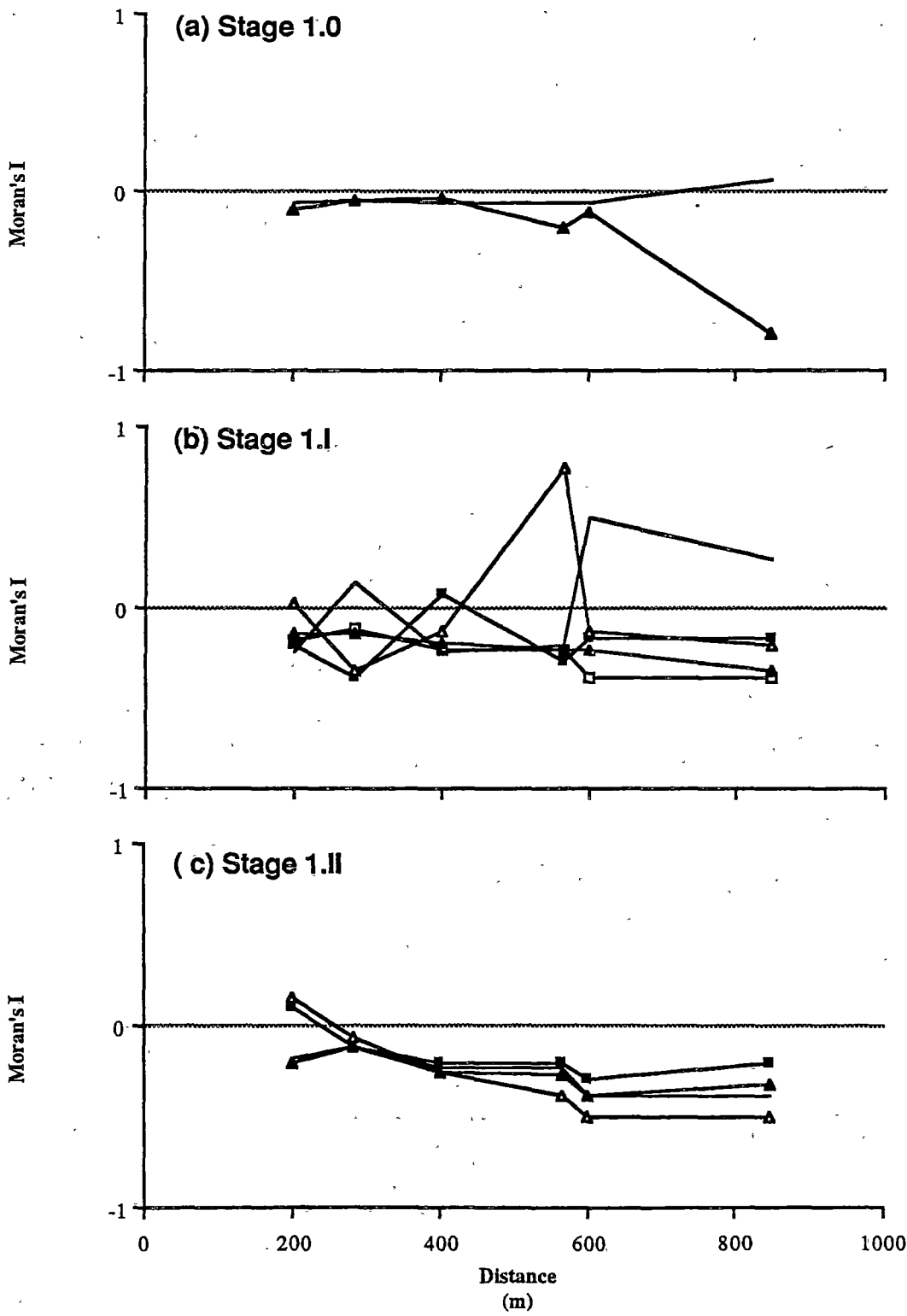
5.2.3 DISPERSAL

For this analysis the age classes in cycle 1, for each trap cell on the grid, were summed over all fly sizes, giving a count of fly numbers in age class per cell and trapping day. Due to the problems outlined above, it was decided that analysis would only be applicable to flies in the first cycle, where the noise introduced by developmental delays would be less than for other cycles. Spatial autocorrelation was performed on this data and the results in the form of correlograms are presented in Figures 5.7 a-f and 5.8 a-f for *L. cuprina* and *L. sericata* respectively. The interpretation of correlograms is described in Section 3.2.2.1.

Lucilia cuprina In stage 1.0 interaction is absent over short distances but there is a tendency towards repulsion between clumps over longer distances. Assuming that mobility is small at the time of emergence and that emergence sites are not clumped then this result indicates that flies are isolated in discrete clumps at this stage. Stage 1.I displays a great deal of variability over all distances, with spatial distribution being more homogenous over the grid. There is still a weak trend to repulsion of clumps. In stage 1.II there is a strong trend from no interaction at short grid distances to weak repulsion between clumps at long distances. Similarly in stage 1.III there is a strong trend, but this is of no interaction over all distances.

Stage 1.IV shows a strong trend of no interaction over short and medium distances, which breaks up and becomes highly variable at long distances. In stage 1.V there is no interaction between flies over short distances, but strong repulsion at medium distances. This is particularly strong for the trapping days after the carcasses were placed in the field and so probably reflects their attraction to flies. This results in concentration of flies at the closest trap sites and thus strong repulsion between clumps. At long distances attraction between clumps is seen.

Figure 5.7. Correlograms of the autocorrelation of age classes against distance for *L. cuprina*.



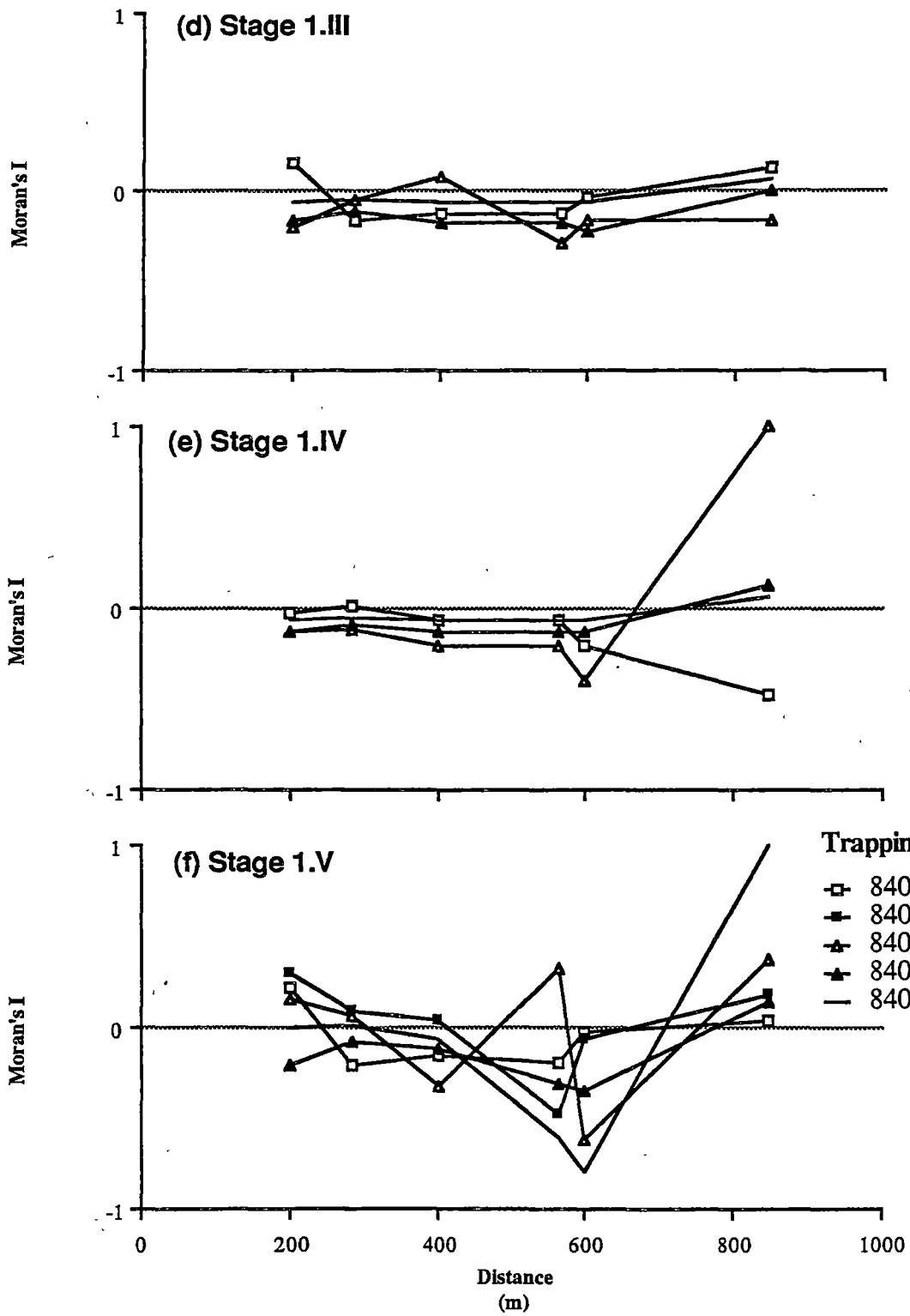
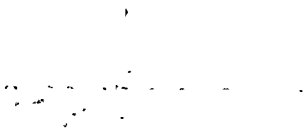
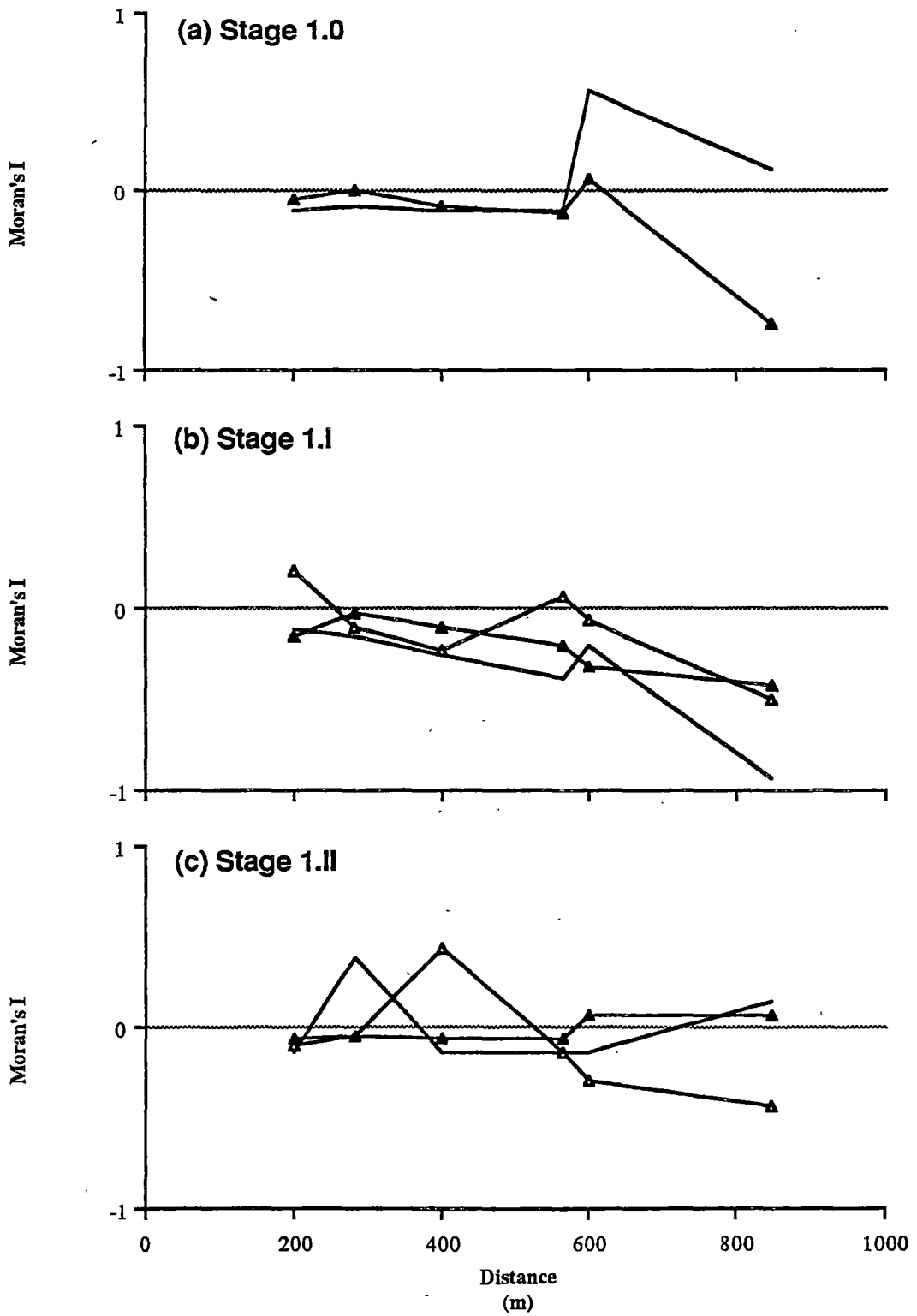
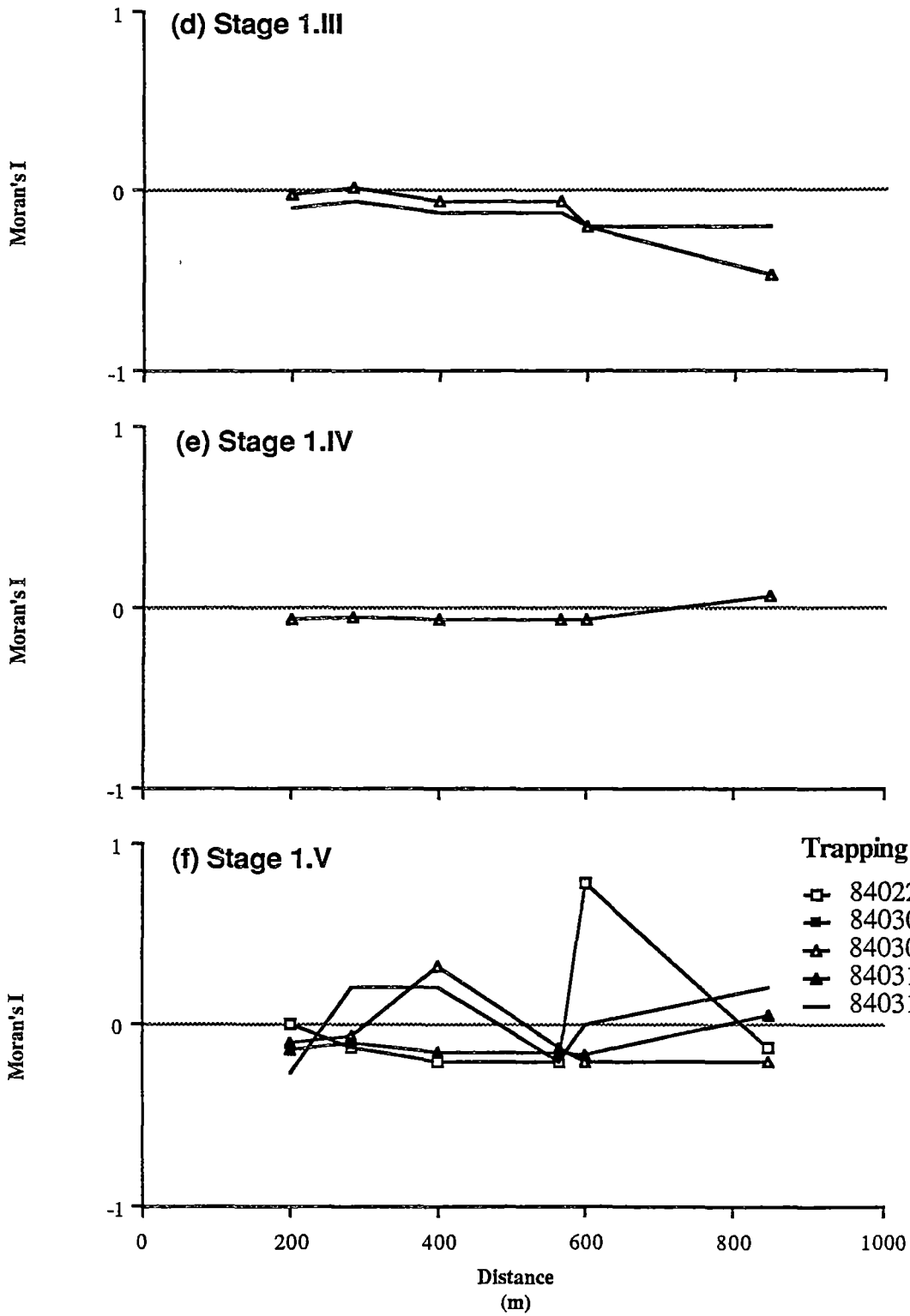


Figure 5.8. Correlograms of the autocorrelation of age classes against distance for *L. sericata*.







Lucilia sericata There is a lot of variation in the spatial distribution of this species by age class, in comparison with *Lucilia cuprina*. In stage 1.0 there is no interaction at short distances. At medium long distances however one trapping day shows strong attraction between clumps whilst at long distances the other trapping day shows strong repulsion between clumps. This variability is unexpected as a strong repulsion between clumps at long distances for newly emerged flies seems to be the most reasonable model. This trend is in fact seen for stage 1.I flies. In stage 1.II there is weak clumping at short to medium distances trending towards no interaction at longer distances.

There is no interaction between stage 1.III and 1.IV flies over all distances. Stage 1.V displays variability from a basic trend of no interaction towards attraction at medium distances. This is not associated with the placement of carcasses.

5.2.4 CARRION EXPERIMENTS

The female fly sizes emerging from the carrion experiments are given in Table 5.1. From this Table it can be seen that *L. cuprina* is reacting to competition. The size range of all females is below that of *low density flies*. The size distribution of *L. sericata* is broader than that of *L. cuprina*, a feature of the size frequency distributions presented in Figure 5.1 b. It is impossible to determine whether the flies of either species emerging from each carcass are from a single cohort. The size distribution for *L. cuprina* in carcass 3 is however quite narrow, suggesting that all the flies experienced a similar amount of competition during the larval period.

Size class (mm)	<i>L. cuprina</i> at carcass number			<i>L. sericata</i> at carcass number		
	1	2	3	1	2	3
2.3			1			
2.4		1	5			
2.5	1		6			
2.6			9			
2.7			9	1		
2.8		1	6	3		
2.9			5			
3.0			1	8	1	1
3.1				9	2	
3.2				13	4	1
3.3				17	2	2
3.4				11	2	5
3.5				7		14
3.6				4		4
3.7					1	1
3.8						1
3.9						
4.0						1
Total	1	2	42	73	12	30

Table 5.1. Size distribution of female flies emerging from carrion field experiments.

5.2.5 INDEX OF REPRODUCTIVE SUCCESS

The signs of resorption of eggs are visible in stages I and II immediately following the stage V at which a failure to find a suitable oviposition site occurred. It cannot then occur in stages 1.I and 1.II as no egg formation preceeds these stages. As an index of the failure of the gravid population to oviposit the frequency of resorbing females in all cycles was calculated by the following calculation for each size class.

$$P_r = (\sum R_{I,II} / \sum N_{I,II}) \times 100$$

where P_r is the proportion of resorbing females in any size class,

$\sum R_{I,II}$ is the total number of females resorbing in all egg cycles,

and $\sum N_{I,II}$ is the total number of females in stages I and II of all post-egg laying cycles (ie discounting cycle 1). The results of this are presented in Table 5.2.

Size class (mm)	P_r for <i>L. cuprina</i> resorbing on trapping day					P_r for <i>L. sericata</i> resorbing on trapping day				
	260384	030384	050384	110384	170384	260384	030384	050384	110384	170384
2.5					0					
2.6										
2.7			50	0					0	
2.8					0				0	
2.9			0					0	50	
3.0				20	0				33	
3.1			33	50				0	50	
3.2	50	0	50	27	17	0		0	67	100
3.3	100	0	100	45	38	100		0	57	0
3.4	0	100	33	30	50			14	100	67
3.5	100	0	50	49	44			20	56	100
3.6	0	100	22	48	50			0	55	0
3.7	0	0	57	40	25			14	43	20
3.8		0	100	56	67			0	61	88
3.9				100		0		100	78	100
4.0							100	33	67	0
4.1									55	100
4.2								100	60	50
4.3								100	100	

Table 5.2. Percentage by size class of female flies resorbing.

It can be seen that the number of resorbing females in both species is a significant proportion, over all size classes. The condition is also manifest on all trapping days. To examine the effects of size on P_r , the mean value of P_r was calculated for each size class for the season total. The data was analysed using linear regression and the results are presented in Figure 5.9 a and b. The fitted regressions were,

$$P_r = 48.964 TI - 128.616$$

$$r_{(2),13} = .789, (P < 0.001) \quad \text{for } L. cuprina$$

$$P_r = 41.618 TI - 109.493$$

$$r_{(2),15} = .825, (P < 0.001) \quad \text{for } L. sericata$$

where TI is thorax length in mm.

In both cases a highly significant positive relationship exists between fly size and susceptibility to resorption. In Section 4.2.1.2. it was shown that flies reared under greater densities had a longer developmental period from emergence to the end of stage 1,V. Thus for a given period the development rate through a gonadotrophic cycle is faster for large flies. If opportunities for oviposition are severely limited then the developmental delays will tend to accumulate large flies more frequently in stage I and II as resorbing females.

To derive P_r the number of resorbing stage I and II flies have been compared with all post egg-laying stage I and II flies. So far in this analysis they have been treated as comparable. The developmental delay caused by resorption will however mean that resorbing flies of stage I or II are physiologically older than nonresorbing stage I or II flies. The higher mortality rates acting on small flies (equation 17, Section 4.2.1.2) is likely to distort the index P_r by producing a relatively greater reduction in small resorbing flies than for large flies. Thus the index P_r would tend to be low for small flies and higher for large flies.

The degree to which these two factors account for the relationship between size and resorption is impossible to assess here. However there can be no doubt that shortages of oviposition sites occur. Given that larger flies have a greater dispersive ability one would expect them to be more capable of detecting and finding widely spread protein sources. This factor alone should affect the relationship seen. That it does not, indicates that the lack of oviposition sites is widespread and severe.

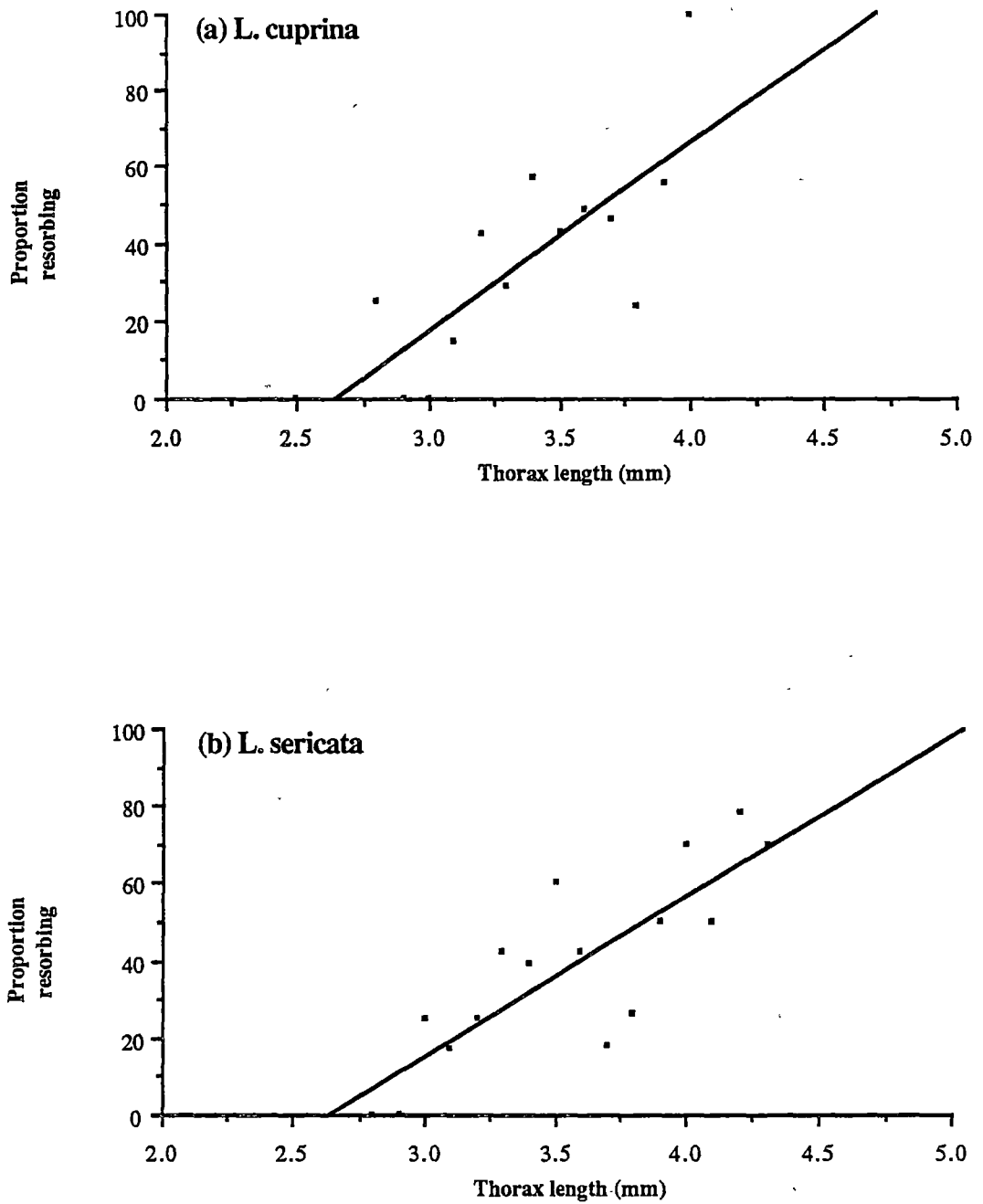


Figure 5.9. The relationship between thorax length and the proportion of females resorbing eggs for *L. cuprina* and *L. sericata* with linear regressions fitted.

5.3 DISCUSSION

5.3.1 THE RELATIVE IMPORTANCE OF LARVAL HABITATS

In this section *high density flies* have been equated with those emerging from carrion. Given the results of the experiment described in the previous chapter, this does not seem to be unreasonable. In that chapter it was demonstrated that small flies are unlikely to originate from myiasis. It should be noted that the property on which these trials were based practiced modern management techniques, such as radical mulesing. Overtly struck sheep would have been quickly dealt with. Myiasis on this type of property is then most likely to be of the covert type (Vogt and Woodburn, 1979).

In covert strikes the density of flies is low enough to limit the area of infestation and thus make detection difficult. The host also does not show the same type of stress associated with an overt strike. It is most likely that this type of strike would give rise to large flies (more so than the flies reared in the artificial myiasis experiments). In carrion, larval densities are more variable and so the range of possible adult sizes covers the size range of the species. The results of the carrion experiments in this study were small adults of *L. cuprina* in low numbers.

The proportion of the fly population attributable to carrion calculated here is based on very crude reasoning. However, given the probable effect of different larval habitats on fly size it would seem to be a useful first estimate of the relative importance of those habitats. The importance of carrion as a possible source of *L. cuprina* has been supported by other authors (Norris, 1959; Kitching, 1981). That the proportion should be so high (18%) is however surprising.

The size distributions of *L. sericata* seen here suggest that it is either less affected by larval density and interaction in carrion, or ^{is} also emerging from myiasis. Norris (1959)

noted that body size of *L. sericata* was more variable than for *L. cuprina* but did not attribute this feature to any environmental factor. Watts *et al.* (1976) found a high incidence of *L. sericata* in strike in Tasmania (45%) but only when *L. cuprina* was also present.

5.3.2 COHORT SEPARATION

Hughes and Nicholas (1974) recognised cohorts of *M. vetustissima* by head width distributions. The size of *M. vetustissima* is governed by food quality rather than quantity, and was used in their study as a means of identifying differences in regional origin of the flies. In this study it was hoped to use size as an indicator of adult origin within a small area. The data showed no obvious polymodality and was therefore difficult to use in isolation.

The use of size and age as separators of cohorts is a novel technique. However it did not prove to be useful. The problem was due to the noise introduced to ovarian age. The source of this noise was attributed to developmental delays (Vogt *et al.* 1974) and differences in emergence times (Foster *et al.*, 1975). As in this study, Vogt *et al.* (1974) found that field samples indicate that females rarely complete the third gonadotrophic cycle. Whitten *et al.* (1977) found that the mean number of cycles completed in the field is generally less than one.

The cohort analysis performed here was time consuming and thus a logistically expensive operation. Due to the problems involved it is not worth pursuing this technique, even on larger data sets.

5.3.3 DISPERSAL

The general dispersal pattern of *L. cuprina* seen here is one of isolated clumps at

emergence, with a tendency to scattering in the egg production stages, followed by attraction to oviposition sites in the egg laying stage. This work related to a maximum scale of 800m and is only sensitive to the relative distribution of size classes.

Barton-Browne (1979) found that the capacity for flight of *L. cuprina* increased in the first few days after emergence. During this time the motivation to react to protein odours increases also (Barton-Browne *et al.*, 1976). The clumping of emerging flies is supported by Vogt and Woodburn (1979), who found a correlation between *L. cuprina* and favourable breeding sites, reinforced by a low tendency to disperse. Mechanisms for the clumping of flies from myiasis have already been discussed (Smith, *et al.*, 1981).

5.3.4 REPRODUCTIVE SUCCESS

Protein sources are important for several key functions of *L. cuprina*. Not only are they integral to the successful formation of eggs (by providing protein meals) and the deposition of eggs at oviposition, but also to mating (Barton-Browne *et al.*, 1976; Woodburn and Vogt 1982). If protein resources are scarce in the field environment then all these factors will be affected (Kitching 1977).

That protein resources may be limited has long been recognised (Wardle, 1930; Norris, 1965; Kitching, 1977). This study has demonstrated that during the trapping season a significant level of egg resorption occurred and this is related to lack of oviposition sites (Webber, 1955; Norris, 1965). Whilst the level of resorption is affected by size, the general level is approximately 40-50% of the egg laying population. This represents a significant amount of egg wastage.

Kitching (1977) concluded from his laboratory experiments that protein shortages and the ensuing delays in egg formation would be important in suppressing the potential

field fecundity of *L. cuprina*. Resorption is a means of conserving protein, which is probably reused in the next gonadotrophic cycle. Clift (1972) concluded that the oogenic strategy of the flies is to develop as many follicles as possible in one cycle. Egg resorption guarantees enough protein for some egg production without any further protein meals in the next cycle. In this way the fly is able to maximise its chances of oviposition when protein is scarce.

5.3.5 GENERAL DISCUSSION

Given the number of *high density flies* (from carrion) and the level of protein shortages seen in the field, what is the importance of carrion to *L. cuprina*? The proportion of *high density flies* in the field population suggests that carrion may be an important source of flies, whilst the shortage of oviposition sites as indicated by the level of egg resorption suggests that carrion would be an attractive alternative oviposition site.

In previous Chapters we have seen that due to the seasonal distribution of species in Tasmania, conditions in carrion may be less hostile to the development of *L. cuprina* than those occurring on the mainland of Australia. In a carrion experiment in the absence of *Chrysomya rufifacies* up to 30% of the emerging flies were *L. cuprina*.

Flies from carrion are likely to be smaller and less numerous than the majority of the field population. As the occurrence of oviposition sites is unpredictable, an individual female has a defined probability of finding one. The probability of successful exploitation is maximised by both the production of many small flies and their relatively high fecundity. Thus carrion could be an important factor in the persistence of a population as *L. cuprina* can use it to provide some small forms to the population. The relationship between size, fecundity and survival will be examined by simple modelling in the next Chapter.

5.4 CONCLUSIONS

- (i). Approximately 18% of the field population of *L. cuprina* is probably derived from carrion.
- (ii). Cohort separation based on adult size and ovarian age is not possible given the errors that can be introduced to physiological age.
- (iii). For *L. cuprina* stage 1,0 flies were clumped as were stage 1,V, the latter being associated with large protein sources (carcasses). All other cycle 1 stages were generally evenly distributed.
- (iv). For *L. sericata* the stage 1,I flies were clumped with other stages more or less evenly distributed. Stage 1,V flies showed little attraction to the carcasses.
- (v). The size distribution of *L. cuprina* emerging from carrion reflected high larval densities and/or interaction with other species.
- (vi). The proportion of resorbing flies of both *L. cuprina* and *L. sericata* were significant, and in the order of 40-50% of the egg laying population.
- (vii). Susceptibility of resorbtion appeared to be highly correlated to adult size, but may reflect physiological effects rather than ability to find suitable oviposition sites.
- (viii). The degree of resorbtion appears to indicate a severe shortage of suitable oviposition sites.

CHAPTER 6.

SIZE EFFECTS ON FITNESS IN AN IDEAL POPULATION.

6.0 INTRODUCTION

In the previous chapters it has been demonstrated that many of the factors restricting *L. cuprina* to myiasis on the mainland of Australia are not relevant or as effective in Tasmania. It was concluded that carrion may have more than a marginal role in contributing adults to the field population.

To assess the degree of this contribution, the response of *L. cuprina* to varying larval densities was measured in laboratory experiments, and the flexibility of adult size with competition was examined. In these experiments *L. cuprina* demonstrated a degree of flexibility in the resultant adult size as a compensation to preadult mortality. The effect of adult size on other life history parameters such as egg batch sizes, development rates and survival were also measured.

The field study described in Chapter 5, showed that oviposition sites were severely limited in the field, as indicated by the number of females resorbing. This led to the suggestion that the population would be more likely to persist if it was composed of many reproductive individuals regardless of their fecundity, rather than of a few highly fecund individuals. This strategy was based on the need to maximise opportunities to find and exploit suitable sites as they became available. Population persistence would then be a function of the number of individuals, their potential fecundity and survival.

The role of carrion breeding as a source of *L. cuprina* has been discounted in the past due to the small number of flies emerging, or the small sizes of flies emerging

(Mackerras, 1936; Waterhouse, 1947; Foster *et al.*, 1975). The smaller forms are in this way equated with less fit forms and their potential contribution ignored. But whilst small flies have a reduced survival and egg batch size, they contribute numerically to the population and so increase the probability of an individual finding a suitable larval habitat.

In Section 5.2.1 it was found that a large component of the field population probably originated in carrion. Given that the proportion of small flies in a field population is large, the relative fitness of these individuals should be assessed, to understand their significance in the persistence of the population properly.

In this Chapter the results of the laboratory experiments described in Chapter 4 are used to produce some simple models to examine the effects of size and the size related changes in life history parameters on the reproductive fitness of the ensuing adult population.

6.1 THE MODELS

6.1.1 POTENTIAL EGG PRODUCTION WITH NO DEVELOPMENTAL DELAYS

The aim of the model developed here is to produce a set of relationships which would describe the relative egg production of flies reared from a fixed substrate size but with a varied competitive regime. This would give the range of adult sizes and the expected number of adults emerging. Fitness, for the purposes of this analysis, is equated with potential fecundity of the individual and the potential number of eggs produced per gram of larval food. Equations referred to in square brackets can be found in Section 4.2.1.2.

Starting with a 10g MRM (1.42g dry weight) larval substrate the density of larvae needed to produce the desired mean female size was calculated (from the consumption rate required, calculated using equation [13]). Larval growth was assumed to take place at 35°C, to simulate either carrion or myiasis.

To simulate density dependent mortality a regression relating density to survival was needed. The data presented in Table 4.1 give larval survival against density, (see Figure 6.1a). Density was transformed to natural logs to linearise the data, and a linear regression was fitted. The results of this analysis are presented in Figure 6.1b. The regression yielded was

$$S_{(1)} = 0.282\ln(D) + 1.427$$

$$r_{(2),23} = 0.834, (P < 0.001)$$

where, $S_{(1)}$ = survival from egg to emergence and D is initial larval density in larvae per gram MRM.

The number of emerging females was computed by calculating the expected sex ratio from equation [19] and multiplying by the number of survivors. Adult development was assumed to occur at 20°C. The size dependent developmental rate through the first gonadotrophic cycle, and subsequent cycle was calculated from equation [10]. Time to the beginning of stage V (all cycles) was taken from the schedule presented by Vogt *et al.* (1974). This schedule assumed a developmental zero for ovarian development of 11.3°C. These schedules were adjusted for size dependent lags by using the correction described above.

Field survival is considerably less than that of laboratory reared flies. To account for this the simulation assumed that all flies died before stage 3.V. From the previous laboratory experiments a multiple linear regression for survival against time, temperature and size (equation [17]) had been derived. It was desirable to accommodate this regression in the model due to its description of temperature and size effects on mortality, however it acted on the laboratory time scale for fly survival. To force it to act under the assumption of total mortality by stage 3.V, the time scale of the simulation had to be standardised to the laboratory time scale. This was done simply by calculating the day on which 50% of the simulation flies and the laboratory flies of a given size and at a given temperature would be dead. The proportion of laboratory days to simulation days was used to correct the logit regression, equation [17].

Batch sizes were calculated with the allometric relationship given in Section 4.2.1.1, and egg production by the survivors at each egg laying time was summed. At the end of the simulation the total egg production, number of females produced, total batches produced and eggs produced per day were output.

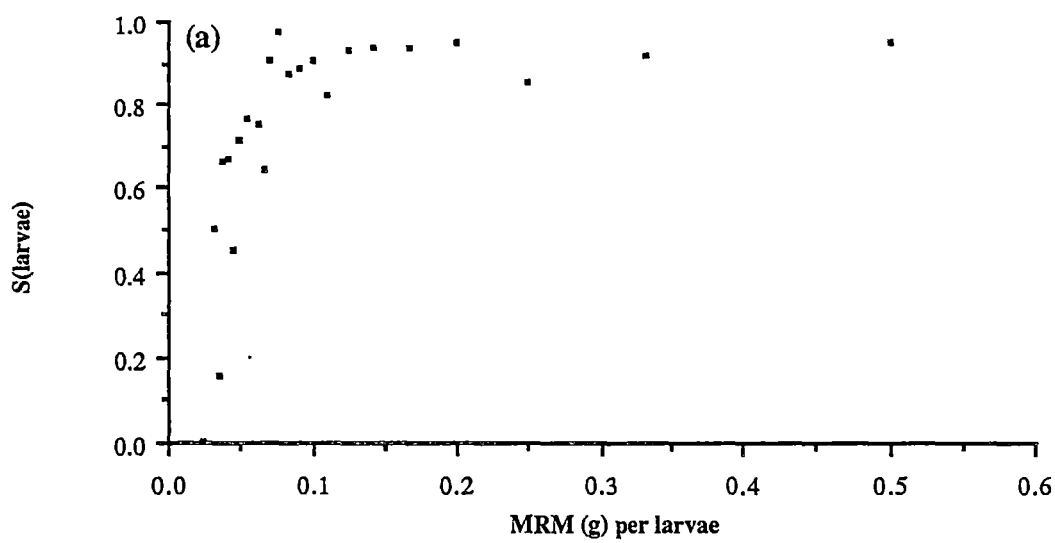


Figure 6.1(a). Relationship between larval survival (from egg to pupa) to larval density, for cultures at 20°C.

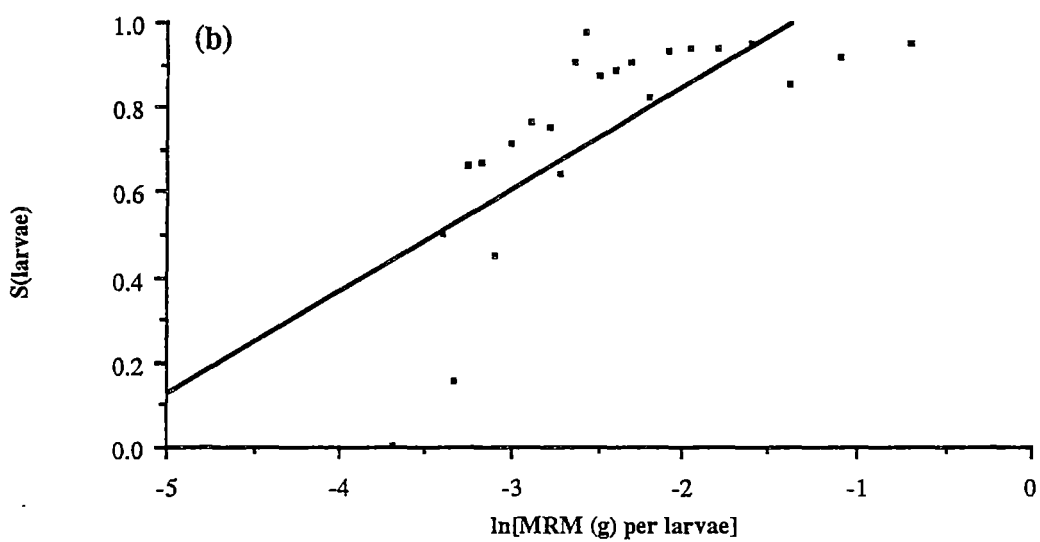


Figure 6.1(b). The same data as in Fig 6.1(b) with density transformed to natural logs and with a linear regression fitted.

The resultant model is given in Appendix 1(a), written in MBASIC.

6.1.2 POTENTIAL EGG PRODUCTION WITH DEVELOPMENTAL DELAYS

To simulate developmental delays induced by shortages of oviposition sites, the regression relating size to proportion resorbing seen in Section 5.2.5 was added to the model. In doing this it was assumed that a delay lasted until the next egg laying period. As the model assumes total mortality by stage 3.V this only effects stages 1 and 2.V.

The lines added to the model are given in Appendix 1(b).

6.2 RESULTS

6.2.1 NO DEVELOPMENTAL DELAYS

The results of the simulation are presented in Figures 6.2 a-e. Calculations were made over the thorax length range of 2.65-4.55 mm. This was to minimise errors in the extremes of the regressions. In Figure 6.2a the expected number of batches per female emerging is plotted against thorax length. It can be seen that the number of batches produced by females of all sizes does not vary greatly (range of 0.73-0.71 with increasing size). The number of females produced from the fixed quantity of larval substrate does however vary greatly (Figure 6.2b). In this case the reduction in adult size is accompanied by a four-fold increase in the number of females produced.

The increased number of females with decreased size increases the total batch output of small flies over the expected life span relative to the larger females (Figure 6.2c). Batch size of the smallest females in this simulation is approximately 85 eggs, whilst the largest is approximately 202 eggs. In consequence when batch output is converted to potential egg production, as in Figure 6.2d, the magnitude of the difference between small and large flies is reduced. In this figure, the higher output of small flies relative to large flies is maintained, but the magnitude of the difference is decreased from four-fold to two-fold.

Persistence is a function of reproductive opportunity and survival time. To obtain a useful temporal index of reproductive potential the number of eggs produced per day was calculated. This calculation was based on the maximum days survived for a given fly size. This gives a measure of the flies' reproductive readiness to exploit the occurrence of a favourable oviposition site. The result of this is presented in Figure 6.2e. The two-fold increase in the index with decreased fly size is again the dominant feature.

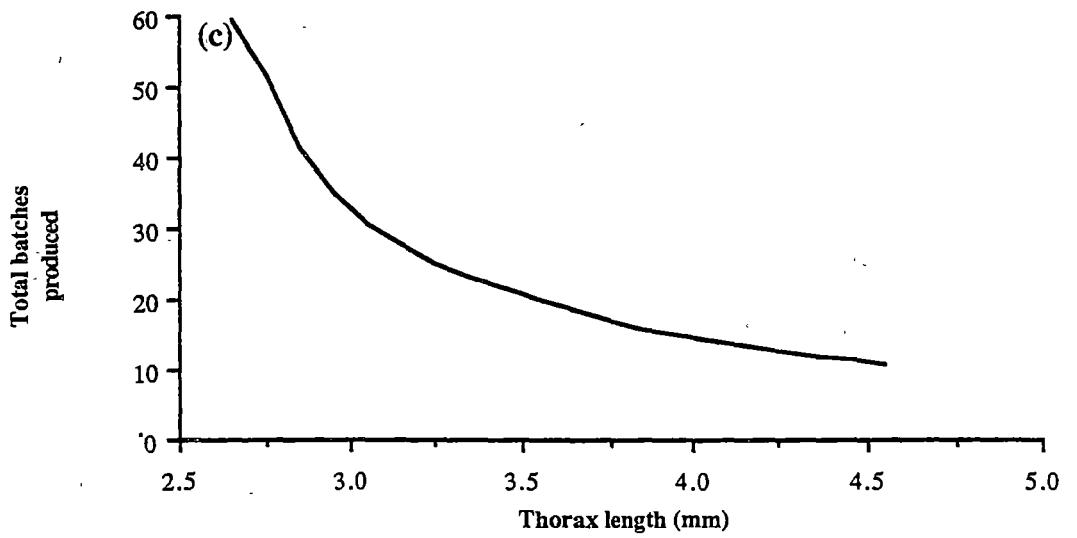
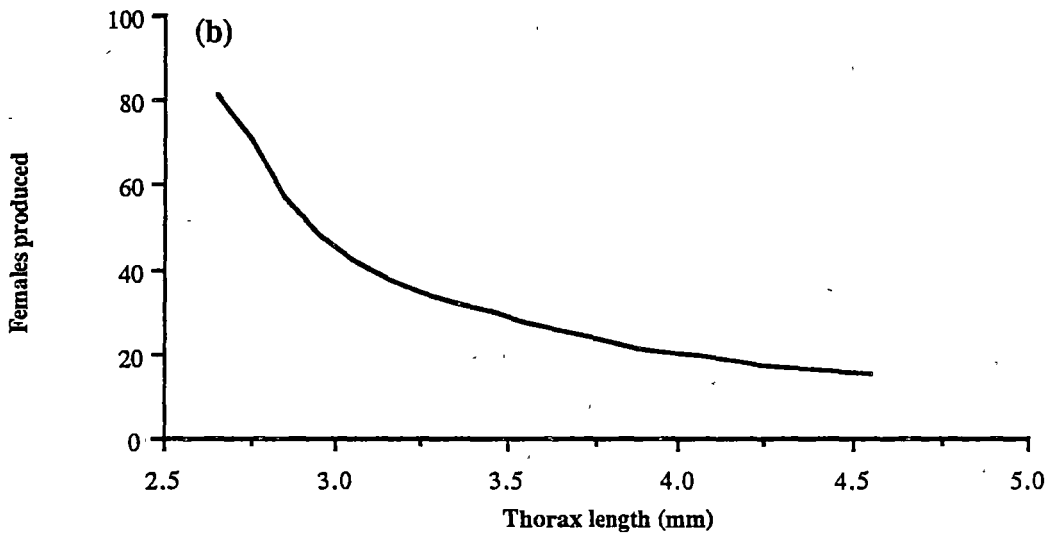
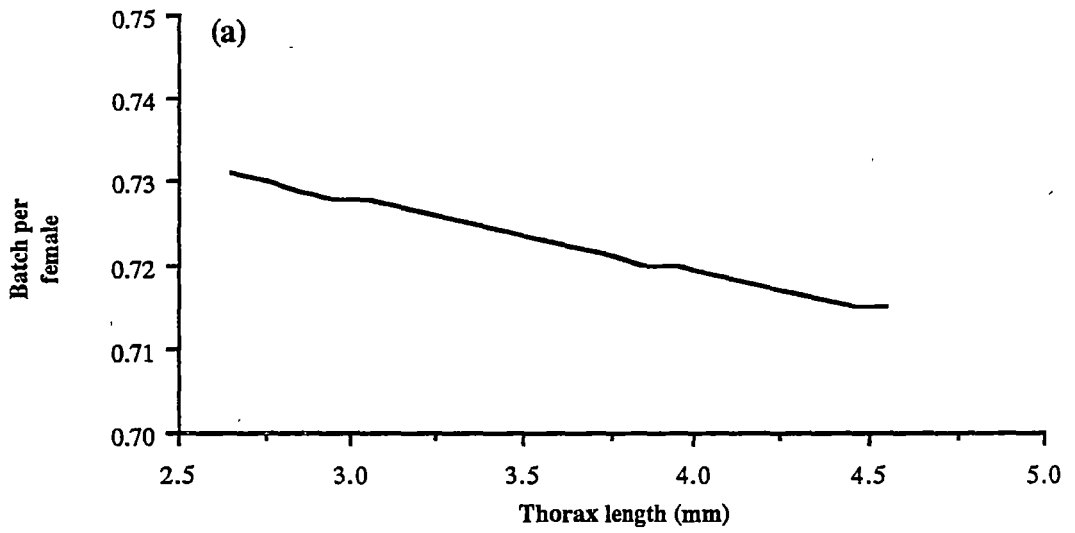
6.2.2 THE EFFECT OF DEVELOPMENTAL DELAYS

The number of females produced in this simulation are the same as for that described above. Developmental delays were assumed to affect eggs produced in both stage 1.V and 2.V. Thus in the following discussion and Figures, batch and egg production refer to effective egg production. This distinction is necessary as delays only reduce egg production by causing degeneration of eggs *in utero*. The egg production for the first cycle would then be unaffected. Females finding suitable oviposition sites would go on to develop normally through cycle 2. The eggs produced but not laid due to protein shortages would then be resorbed and the subsequent cycle delayed. The eggs destined to be oviposited normally are treated here as effective eggs.

The results of the simulation are presented in Figures 6.3 a-e. Developmental delays from the regression derived in Section 5.2.5, are greater on large flies than small flies. This basic relationship exaggerates the results of the simulation without delays described above. No changes (other than magnitude) occur in the relationship of the major variables. Batch production per female (Figure 6.3a) covers the range 0.70-0.03 with increasing adult size. The difference in batch production between small and large flies (Figure 6.3b) is in the order of six-fold decrease with increased size. Similarly egg production for small flies is three times greater than that of the larger flies (Figure 6.3c).

Egg production per adult shows a reversed trend to that of the allometric relationship (Figure 6.3d). Effective egg production of the largest flies is almost 0.05% of the potential production. The index of egg production per day shows a four-fold increase with decreased size (Figure 6.3e).

Figure 6.2(a-e). Output from the simulation of potential egg production with no developmental delays.



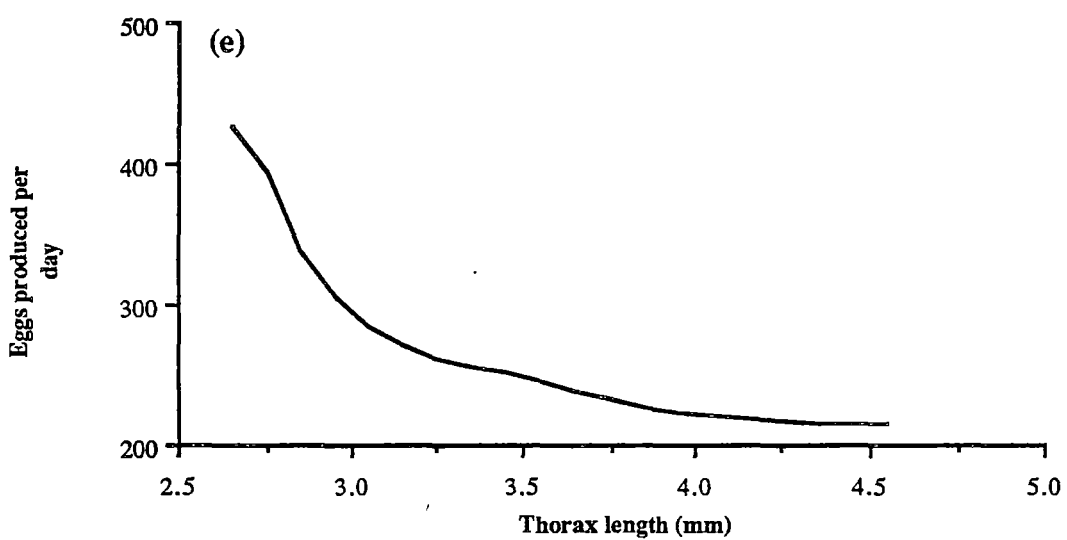
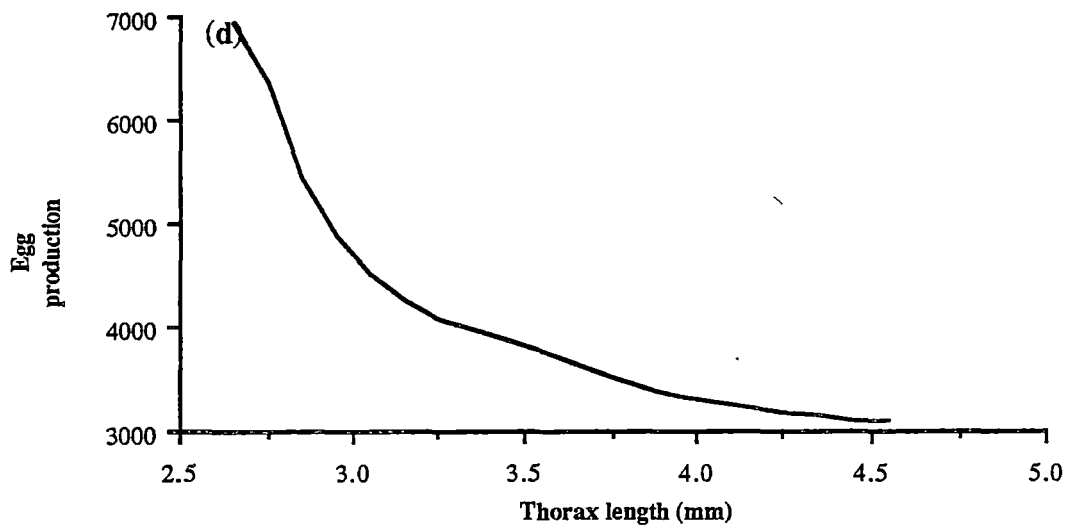
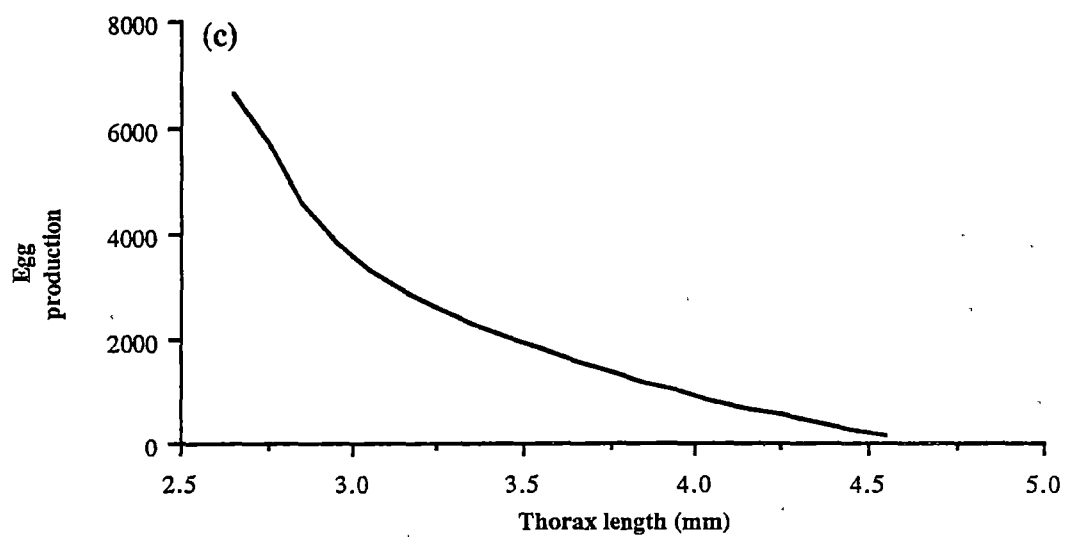
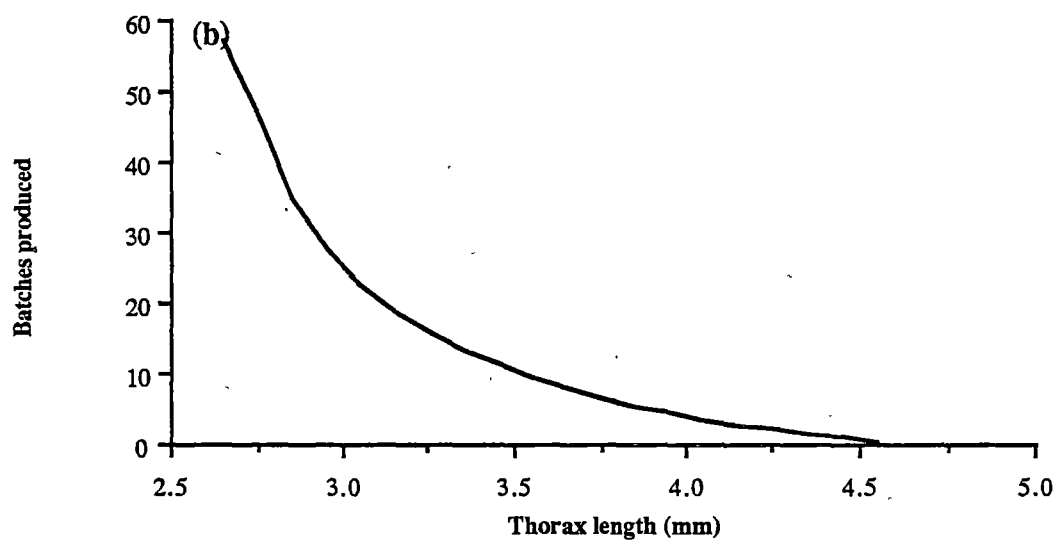
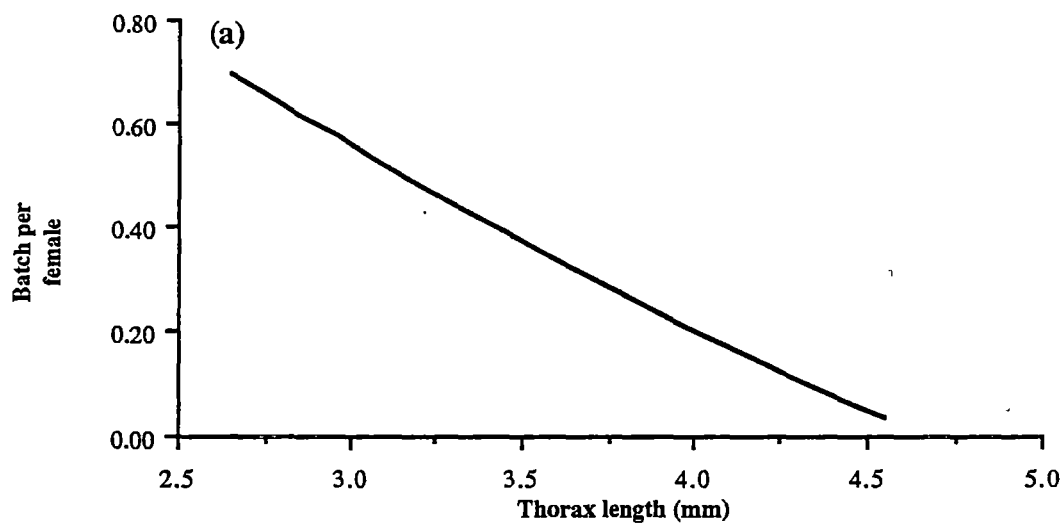
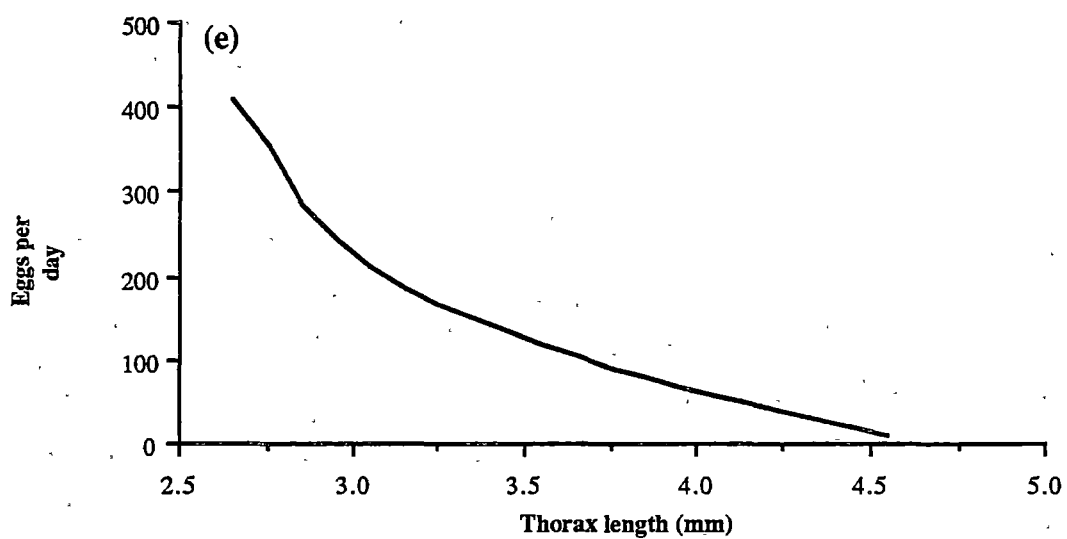
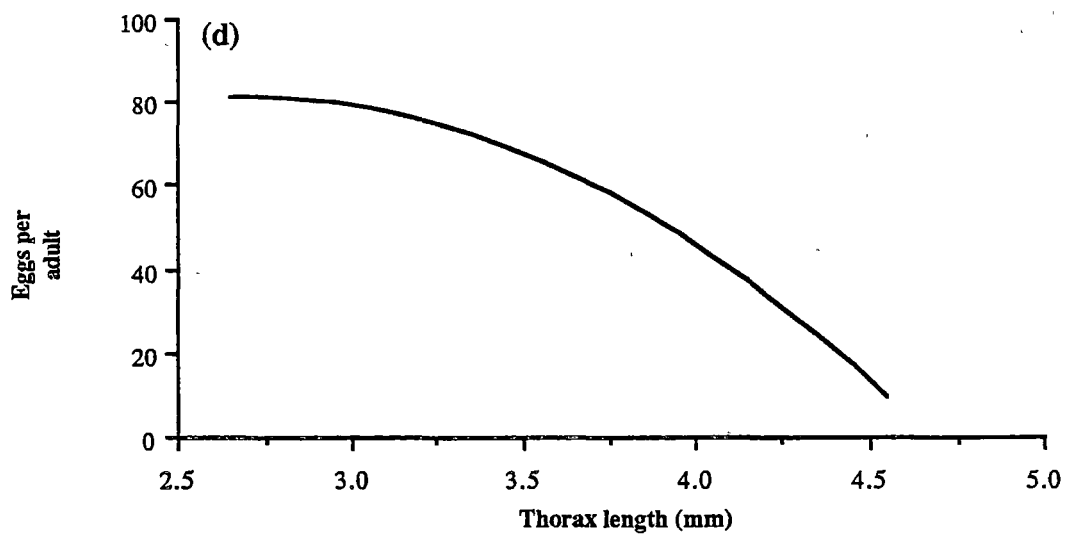


Figure 6.3(a-e). Output from the simulation of potential egg production with developmental delays.





6.3 DISCUSSION

It does not seem reasonable to assume that the reproductive fitness described here is the only measure of fitness for adult *L. cuprina*. If that were the case then there would be no selective pressure on *L. cuprina* to maintain the range of possible adult sizes that it displays. Rather it would be to the flies' advantage to optimise their development at smaller sizes. Since this is not the case, it suggests that an important set of variables has not been accounted for. The most apparent deficiency in the model is the lack of a description of the effects of size on the probability of finding key resources.

Kitching (1977) concluded that shortages of protein resources could suppress potential fecundity in three ways. These were

- i), to reduce the amount of protein available to females and so stop egg development,
- ii), to deny gravid females oviposition sites and so force them into the resorption cycle,
- and iii), to limit opportunities for mating.

The third factor listed above relates protein sites to mating sites. When protein was limited, the proportion of unmated gravid flies increased, suggesting that mating was reduced by the inability of flies to find mates.⁵ This mechanism originally suggested by Barton-Browne *et al.* (1976) is supported by field observations made by Woodburn and Vogt (1982).

In all the cases listed above, the fly must take an active role in searching for the necessary resources. If size has an affect on the ability of flies to find resources then this would directly effect the potential egg production. No studies of size effects on dispersal have been made for *L. cuprina*, apart from a theoretical model given by Williams and

Richardson (1983) based on the flies energetics. In this study it was suggested that with decreased adult size more energy was allocated to reproduction, and consequently less to dispersal. Roff (1977) in a similar study on *Drosophila spp.* found that the energetic and reproductive costs of dispersal decrease with increasing size.

If ephemeral protein resources occur randomly, both spatially and temporally, then smaller flies are less likely to find resources than large flies. This would be due to the difference in dispersal strength and thus searching ability with fly size. That is, to obtain resources flies must actively search for them, and thus the most active are most likely to be successful. This however is not indicated by the relationship determined in Section 5.2.5 between size and frequency of resorption. Some factors were suggested in that Section which would decrease the scale of the relationship but some correlation still remains.

A possible mechanism which may explain the phenomenon seen in the simulations is that resources are not randomly distributed, under this model changes in individual reproductive fitness may represent bet-hedging. That is, the larger forms represent the dispersive form of the population and the smaller individuals, the persistent form. As adult emergence sites are concentrated by the host, then sedentary forms are likely to have some opportunity to find suitable resources due to the positive correlation of host and parasite. The larger forms, with a lower reproductive fitness represent a gamble between wasted reproductive effort and active searching for new larval habitats. A by-product of this strategy is that a population undergoing shortages of larval habitat would persist locally with its reproductively fittest forms (due to their more sedentary habit).

Nicholson (1950) concluded from his observations on larval survival that killing a high percentage of flies in the field would not necessarily reduce their eventual abundance. In a refinement of this argument, Collins (1980) conclude that the sacrifice of adult size to

compensate for larval mortality indicated that minimising prereproductive mortality was critical to the species survival. He also found that the investment of energy in the young (that is the size of eggs) was at a minimum for survival and optimised the female fecundity. That egg size was unaffected by adult size led him to conclude that a maximal output of propagules was also critical. These two factors maximise the numerical size of the population and its reproductive potential, regardless of its dispersive ability.

A consequence of maximal population size is the overexploitation of resources when they become available. In the case of myiasis it has been demonstrated that no overcompetition occurs. However, no correlation exists between carcass size and the number of eggs laid (Putman, 1977), so it is probable that overcompetition is common in carrion, and compensated for to some degree.

In all the cases discussed above the idea of an optimal size is irrelevant. Roff (1981) found that wide variation in life history parameters of dipterans had minimal effects on optimum body size. This was due to the difficulty in defining an optimum size when a range of sizes was a natural consequence. The effects of size on fitness were usually accommodated by other factors resulting in individuals with similar fitnesses over a wide range of phenotypes.

6.4 CONCLUSIONS

- (i). Reproductive fitness as expressed by the potential production of eggs by flies emerging from a constant substrate size is maximised in the smaller forms of *L. cuprina*.
- (ii). Developmental delays as simulated with the regression derived in Section 5.2.5, exaggerates this relationship.

CHAPTER 7.

GENERAL DISCUSSION.

7.0 INTRODUCTION

This study has set out to assess the effects of competition on *Lucilia cuprina* with particular reference to the success of this species in carrion breeding in Tasmania. The spatial and temporal interaction of the necrophagous fly guild was studied in the main sheep raising areas of the state. It was found that *Chrysomya rufifacies* and *Chrysomya varipes* had a restricted distribution both geographically (occurring in the northern and central areas of the state) and seasonally (first occurrence being usually in mid- to late summer).

Ch. rufifacies is a major predator of *L. cuprina* and other larvae in carrion, and its absence during the periods of peak abundance of the sheep blowfly suggested a possible loosening of the constraints suppressing this species success in carrion in other eastern Australian states. This contention was tested with a carrion study in the presence and absence of *Ch. rufifacies*. In the absence of *Ch. rufifacies* some *L. cuprina* were seen to emerge from carrion. The temperatures generated within a carcass were monitored and although high temperatures were generated these were within the thermal tolerance of *L. cuprina*. There was no correlation between the abundance of species emerging and the abundance of species trapped adjacent to the carcasses.

The fine scale distribution of *L. cuprina* was found to be highly correlated with the presence of both live sheep and sheep carcasses. It had a strongly clumped distribution with several strong nodes of abundance within the trapping area (1km² of sheep pasture). A high proportion of the population was found to be resorbing eggs and this was assumed

to indicate a severe shortage of suitable oviposition sites.

Due to the possibility that *L. cuprina* breeds in carrion (from the experiments described above), a laboratory study was conducted to simulate competition in both carrion and myiasis. This study showed that *L. cuprina* had a considerable capacity for compensating preadult mortality by sacrificing adult size. This reaction and its effects on various life history parameters was studied. Induced myiasis using a range of larval densities commonly found in the field showed that adult size and preadult mortality were independent of initial density.

The flies emerging from the induced myiasis experiments were in the larger range of adult sizes. Flies emerging from the artificial carrion experiments covered the whole range of adult sizes, and there was a strong correlation of adult size to larval density. This observation led to the analysis of the field population for size related effects of competition.

The general size distribution of flies was related to alternative larval habitats, and it was concluded that at least 18% of the population studied originated from conditions of high larval densities and therefore, probably from carrion breeding. To assess the likely effects of larval competition on the reproductive fitness of the adult population a simple simulation model was constructed. This showed that whilst individual fecundity decreased, the potential reproductive output of a cohort was increased with increased competition (and consequently decreased adult size). This result demonstrated that competition occurring in carrion may increase the overall reproductive potential of the flies emerging, although other factors such as mobility (and thus the probability of a successful oviposition) may be reduced.

It was concluded that numerical success was important to the persistence of *L.*

cuprina populations regardless of the size of individuals. Numerical success was seen to be optimised by the compensation of preadult mortality. Carrion breeding as a significant contributor to the persistence of this species has been largely discounted in the past. This has been due to either the presence of *Ch. rufifacies* or the judgement that small flies emerging from carrion made a lesser contribution to the population. The results of this study suggest that the role of carrion breeding needs to be considered more seriously at least in Tasmania and that size effects are an important population characteristic.

7.1 SPATIAL AND TEMPORAL INTERACTION OF THE SPECIES

The spatial distribution of *L. cuprina* seen in this study is in agreement with, and extends, the reports in the literature. The correlation of the occurrence of *L. cuprina* to sheep distribution has been made on a regional scale by Waterhouse and Paramonov (1950). Vogt and Woodburn (1979) in a review article suggested that there may be a finer scale interaction of fly abundance and sheep distribution.

The clumped microgeographical distribution of this species is well known (Norris 1959; Vogt and Woodburn, 1979; Wardhaugh *et al.*, 1983b). Recently it has been determined that sheep camp sites generally yield the greatest concentrations of *L. cuprina* (Wardhaugh, *et al.*, 1983b).

The dominance of *L. sericata* in rural Tasmanian population of blowflies was first reported by Ryan (1954). Its presence in large quantities is confirmed in this and other recent studies (McQuillan, *et al.*, 1983). These studies have also demonstrated the limited distribution of *Chrysomya* spp. in this state. The presence of *L. sericata* has also been linked to its involvement in strike, although its role is one of opportunist rather than initiator, (Watts *et al.*, 1976) [it was only recorded in association with *L. cuprina* in strikes].

The interaction of the two species of *Lucilia* remains to be resolved, and may prove to be important in the biological control of the economically important species.

7.2 EFFECTS OF COMPETITION ON POPULATION DYNAMICS

Using the analysis of Collins(1980), it can be surmised that the flexibility in adult size maximises survival. The concomitant change in batch size can be assumed to be less essential to fitness. This is confirmed in this study by demonstrating that with decreased batch size the overall reproductive potential of a cohort is increased. Williams and Richardson (1983) found that the ratio of reproductive tissue to other body tissues increases with decreased size. This was assumed to reduce mobility due to the lower possible energetic contribution to flight. This in turn suggests that dispersive ability is of lesser importance than survival and reproductive potential.

Both *L. cuprina* and *L. sericata* are relatively sedentary [Kitching (1981) and Cragg (1955) respectively]. The spatial association between flies and sheep is also reinforced by the nature of larval drop-off from myiasis (Vogt and Woodburn, 1979) and low adult dispersal. Lower mobility is therefore probably not a critical problem for these species, because of clumped nature of the larval resource (Williams and Richardson, 1983).

These factors lead to the conclusion that adult size is not critical in maintaining sheep blowfly populations. Rather, the number of vectors produced is critical. By way of comparison, Denno and Cothran (1975) found that larviparous/ovoviviparous flies were associated with a larger adult size and lower fecundity. These populations could survive at lower densities than oviparous species due to their greater parental investment in the propagules. Larval growth in these species was rapid, and in this way they avoided

interspecific competition.

The laboratory studies of myiasis reported here note that small flies are unlikely to be produced. It should be noted however, that these experiments tested only the outcome under varying levels of intra-specific competition. *L. cuprina* is found in multispecies strikes and this may change the nature and thus the effects of competition.

7.3

AN ASSESSMENT OF THE ROLE OF CARRION BREEDING

There is great geographical variation in the success of *Lucilia* spp in carrion. Its success is largely dependent on the composition of the local guild of necrophagous flies. For example in South Africa, Ulyett (1950) found that *L. sericata* and *L. cuprina* were the best adapted members of the fly guild for scramble competition, and this led to their successful role in carrion breeding. On the eastern mainland of Australia *L. cuprina* is found to be largely unsuccessful, although Norris (1959) suggests that it may contribute to this species persistence particularly in the winter months.

During the course of this study the Second National Symposium on Sheep Blowfly and Flystrike in Sheep was held by the N.S.W. Department of Agriculture. Several papers were delivered which demonstrated that the success of *L. cuprina* in carrion breeding varied in different regions. *L. cuprina* was found to have no significant success in Queensland and the arid zone of N.S.W. (O'Sullivan, *et al.*, 1983 and Anderson, *et al.*, 1983 respectively). In contrast carrion breeding particularly in large carcasses in summer is of importance in Western Australia (Monzu *et al.*, 1983). In this instance carrion breeding is of particular significance as it occurs at a time of year when sheep are not susceptible to myiasis and so this contributes to the populations persistence.

The relevance of carrion breeding to the control of sheep blowfly is difficult to define. Past efforts in carcass destruction were ineffective as carrion could not be found in

time to effectively treat it (Norris, 1959). Furthermore the results presented here demonstrate the effectiveness of strategies displayed by *L. cuprina* to aid the persistence of the species. These strategies make it extremely unlikely that any single biological control measure will be successful in reducing the damage caused by this species.

The most significant and cost-effective control that could be adopted in Tasmania is the wide spread adoption of the radical mulesing operation for non Merino breeds. This operation, with a proven record of protection against flystrike [up to 90% reduction in the occurrence of crutch strike (Jones and McQuillan, 1983)] is still not widely practiced here (Reid and Jones, 1976).

7.4 UNRESOLVED QUESTIONS

This study has left some questions unresolved, and has also raised some issues which require further work. These are as follows.

1. The role of *Lucilia sericata* in rural areas of Tasmania is unknown as is the degree of interaction between adults and larvae of this species and others (principally *Lucilia cuprina*) in the necrophagous fly guild.
2. What are the effects of size on the dispersive ability of *L. cuprina* and how do these affect the inferences drawn in this thesis relating to population persistence?
3. Does the size distribution of the population change when myiasis increases? This would be an interesting test of the hypothesis that *high density flies* originate from carrion. If it were true, one would expect the proportion of large flies to increase with increasing myiasis, whilst the proportion of small flies would remain relatively constant. Conversely an overall increase in the abundance of all sizes would be seen.
4. What are the effects of size on egg resorption rates?

5. Given the nonrandom distribution of oviposition sites and size differences in dispersal ability, what are the optimal strategies for reproductive adults, *i.e.* sessile or vagile?

REFERENCES

- Anderson, J. M. E., Shipp, E. and Anderson, P. J. (1983). Blowfly populations and strike incidence in the arid zone of N.S.W. **In:** The Proceedings of the Second National Symposium *Sheep Blowfly and Flystrike in Sheep*. Dept. Agriculture N.S.W.
- Anon (1930). Recent developments in blowfly research. *Aust. CSIR J.* 3, 212-9.
- Arnold, G.W. and Dudzinski, M.L. (1978). *Ethology of free-ranging domestic animals*. Elsevier Sci. Publ. Co. Netherlands.
- Barton, N.J. (1981). Sheep blowflies of Victoria. *Research Project Series*. 116, Vic. Dept. of Agriculture.
- Barton-Browne, L. (1979). The behaviour and nutritional requirements of adults of *Lucilia cuprina* possibilities for modification. **In:** The Proceedings of the First National Symposium *Sheep Blowfly and Flystrike in Sheep*. Dept. Agriculture N.S.W.
- Barton-Browne, L., Bartell, R.J., van Gerwen, A.C.M, and Lawrence, L.A. (1976). Relationships between protein ingestion and sexual receptivity in females of the Australian sheep blowfly *Lucilia cuprina*. *Physiol. Entomol.* 1, 235-40.
- Barton-Browne, L., van Gerwen, A.C.M. and Williams, K.L. (1979). Oocyte resorption during ovarian development in the blowfly *Lucilia cuprina*. *J. Insect Physiol.* 25,

147-53.

Bedding, R. A. (1983). Susceptibility of *Lucilia cuprina* larvae to parasitization by steinernematid and heterorhabditid nematodes. **In:** The Proceedings of the Second National Symposium *Sheep Blowfly and Flystrike in Sheep*. Dept. Agriculture N.S.W.

Bornemissza, G.F. (1957). An analysis of arthropod succession in carrion and the effects of its decomposition on the soil fauna. *Aust. J. Zool.* 5, 1-12.

Burrell, D. H. (1983). The pathogenesis and immunology of fleece-rot, dermatophilosis and body strike. **In:** The Proceedings of the Second National Symposium *Sheep Blowfly and Flystrike in Sheep*. Dept. Agriculture N.S.W.

Cliff, A. D. and Ord, J. K. (1973). *Spatial autocorrelation* Pion, London.

Cliff, A. D. (1972). *The nutritional and endocrine control of reproduction of the Australian sheep blowfly Lucilia cuprina (Wiedemann)* Ph. D. Thesis, University of Sydney.

Collins, N.C. (1980). Developmental responses to food limitation as indicators of environmental conditions for *Ephydra cinere* Jones (Diptera). *Ecology* 61, 650-661.

Cormack, R.M. and Ord, J.K. (1979). *Spatial and Temporal Analysis in Ecology*. Int. Co-op. Publ. House. Maryland.

Cragg, J.B. (1955). The natural history of sheep blowflies in Britain. *Ann. Appl. Biol.* 42, 197-207.

CSIRO Division of Entomology (1979). *The Insects of Australia : A Textbook for Students and Research Workers*. Melb. Uni. Press

Dallwitz, R. (1983). Apparatus for collecting blowfly larvae leaving struck sheep. *Gen. Appl. Entomol.* 15, 35-6.

Denno, R.F. and Cothran, W.R. (1975). Niche relationships of a guild of necrophagous flies. *Ann. Entomol. Soc. Am.* 68, 741-54.

Drake, V.A., Helm, K.F., Readshaw, J.L. and Reid, D.G. (1981). Insect migration across Bass Strait during spring : a radar study. *Bull. Entomol. Res.* 71, 449-66.

Emmens, R.L. and Murray, M.D. (1982). The role of bacterial odours in oviposition by *Lucilia cuprina* (Wiedemann) (Diptera : Calliphoridae), the Australian sheep blowfly. *Bull. Entomol. Res.* 72, 367-75.

Emmens, R.L. and Murray, M.D. (1983). Bacterial odours as oviposition stimulants for *Lucilia cuprina* (Wiedemann) (Diptera : Calliphoridae), the Australian sheep blowfly. *Bull. Entomol. Res.* 73, 411-15.

Foster, G.G., Kitching, R.L., Vogt, W.G. and Whitten, M.J. (1975). Sheep blowfly and its control in the pastoral ecosystem of Australia. *Proc. Ecol. Soc. Aust.* 9, 213-29

- Froggatt, W.W. (1904). The sheep maggot fly, with notes on other common flies. *Agric. Gaz. NSW.* **15**, 1205-11.
- Froggatt, W.W. (1915). Sheep maggot flies. *N.S.W. Dept. Ag. Farmers Bull.* **95**.
- Fuller, M.E. (1932a). The blowfly problem - notes on the effect of carcass burial. *Aust. CSIR. J.* **5**, 162-4.
- Fuller, M.E. (1932b). The larvae of the Australian sheep blowflies. *Proc. Linn. Soc. N.S.W.* **57**, 77-91.
- Fuller, M.E. (1934). The insect inhabitants of carrion : A study in animal ecology. *Aust. CSIR Bull.* **82**.
- Gherardi, S.G., Monzu, N., Sutherland, S.S., Johnson, K.G. and Robertson, G.M. (1981). The association between body strike and dermatophilosis of sheep under controlled conditions. *Aust. Vet. J.* **57**, 268-71.
- Gherardi, S.G., Sutherland, S.S., Monzu, N. and Johnson, K.G. (1982). Field observations on body strike in sheep affected with dermatophilosis and fleece-rot. *Aust. Vet. J.* **60**, 27-8.
- Gilmour, D., Waterhouse, D.F. and McIntyre, G.A. (1946). An account of experiments undertaken to determine the natural population density of the Sheep Blowfly *Lucilia cuprina*. *Aust. CSIR Bull.* **195**, 1-39.

- Graham, N.P.H. Johnston, I.L. and Riches, J.H. (1947). Studies on fly strike in Merino sheep. 7. The effect of tail length on susceptibility to flystrike in ewes. *Aust. Vet. J.* 23, 31-4.
- Gurney, W.B. and Woodhill, A.R. (1926). Range and longevity of Sheep Blow-flies. *Ag. Gaz. N.S.W.* 27, 49-64.
- Hall, C.A., Martin, I.C.A. and McDonell, P.A. (1980). Patterns of wool moisture in merino sheep and its association with blowfly strike. *Res. Vet. Sci.* 29, 181-85.
- Hanski, I. (1977). An interpolation model of assimilation by larvae of the blowfly *Lucilia illustris* (Calliphoridae) in changing temperatures. *Oikos* 28, 187-95.
- Hayman, R.H. (1953). Studies in fleece-rot of sheep. *Aust. J. Agric. Res.* 4, 430-68.
- Holdaway, F.G. (1932). Fly strike of sheep : A natural phenomenon. *Aust. CSIR. J.* 5, 205-11.
- Holdaway, F.G. and Mulhearn, C.R. (1934). Field observations on weather stain and blowfly strike of sheep with special reference to body strike. *Aust. CSIR. Pamphlet.* 48.
- Hughes, R.D. (1970). The seasonal distribution of bushfly (*Musca vetustissima* Walker) in south-eastern Australia. *J. Anim. Ecol.* 39, 691-706.
- Hughes, R.D. (1974). Variation in the proportion of different reproductive stages of

female bushflies (*Musca vetustissima* Wlk. (Diptera : (Muscidae)) in bait catches as a cause of error in population estimates. *Bull. Entomol. Res.* 64, 65-71.

Hughes, R.D. (1977a). The population dynamics of the bushfly : the elucidation of population events in the field. *Aust. J. Ecol.* 2, 43-54.

Hughes, R.D. (1977b). Some problems associated with quantitative sampling of bushfly (*M. vetustissima* Walker). *J. Aust. Entomol. Soc.* 16, 117-22.

Hughes, R.D., Greenham, P.M., Tyndale-Biscoe, M. and Walker, J.M. (1972). A synopsis of observations on the biology of the Australian bushfly *M. vetustissima* (Walker). *J. Aust. Entomol. Soc.* 11, 311-31.

Hughes, R.D. and Nicholas, W.L. (1974). The spring migration of the bushfly (*Musca vetustissima* Walk.) : Evidence of displacement by natural population markers including parasitism. *J. Anim. Ecol.* 43, 411-28.

Joint Blowfly Committee. (1933). The sheep blowfly problem in Australia. Report No. 1. *Aust. CSIR Pamphlet.* 37.

Jones, A.I. and McQuillan, P. B. (1983). Strike incidence and mulesing in Tasmania. In: The Proceedings of the Second National Symposium *Sheep Blowfly and Flystrike in Sheep*. Dept. Agriculture N.S.W.

Jumars, P.A., Thistle, D. and Jones, M.L. (1977). Detecting two-dimensional spatial structure in biological data. *Oecologia (Berl.)*. 28, 109-23.

Kaplan, R.H. and Cooper, W.S. (1984). The evolution of developmental plasticity in reproductive characteristics : An application of the "adaptive coin-flipping" principle. *Am. Nat.* 123, 393-410.

Kitching, R.L. (1977). Time, resources and population dynamics in insects. *Aust. J. Ecol.* 2, 31-42.

Kitching, R.L. (1981). The sheep blowfly : a resource-limited specialist species. In: Kitching, R.L. and Jones, R.E.(eds) *The Ecology of Pests. Some Australian Case Histories*. CSIRO. Melb.

Kooijman, S. A. L. M. (1979). The description of point patterns. In: Cormack, R. M. and Ord, J. K. (eds.) *Spatial and Temporal Analysis in Ecology* Int. Co-op. Publ. House. Maryland.

Levot, G. W., Brown, K. R. and Shipp, E. (1979). Larval growth of some calliphorid and sarcophagid Diptera. *Bull. ent. Res.* 69, 469-75.

Mackerras, I.M. (1936). The sheep blowfly problem in Australia : Results of some recent investigations. *Aust. CSIR Pamphlet.* 66.

Mackerras, I.M., Fuller, M.E., Austin, K.M. and Lefroy, W.H.B. (1936). Sheep blowfly investigation. The effect of trapping on the incidence of strike in sheep. *Aust. CSIR J.* 9, 153-62.

Mackerras, I.M. and Fuller, M.E. (1937). A survey of the Australian sheep blowflies. *Aust. CSIR J.* 10, 261-70.

- Mackerras, I.M. and Mackerras, M.J. (1944).** Sheep Blowfly Investigations : The attractiveness of sheep for *Lucilia cuprina*. *Aust. CSIR Bull.* 181.
- MacLeod, J. (1937).** The experimental production of cutaneous myiasis of sheep. *Parasitology* 29, 526-9.
- McGuirk, B. J. (1983).** Breeding for increased resistance to fleece rot and body strike. **In:** The Proceedings of the Second National Symposium *Sheep Blowfly and Flystrike in Sheep*. Dept. Agriculture N.S.W.
- McQuillan, P., Jones, A.L. and Williams, H. (1983).** Recent studies on Sheep Blowflies (Diptera : Calliphoridae) in Tasmania. **In:** The Proceedings of the Second National Symposium *Sheep Blowfly and Flystrike in Sheep*. Dept. Agriculture N.S.W.
- Merritt, G.C. and Watts, J.E. (1978a).** An *in vitro* technique for studying fleece-rot and flystrike in sheep. *Aust. Vet. J.* 54, 517-20.
- Merritt, G.C. and Watts, J.E. (1978b).** The changes in protein concentration and bacteria of fleece and skin during the development of fleece-rot and body strike in sheep. *Aust. Vet. J.* 54, 513-6.
- Monzu, N., Gherardi, S. G. and Zentai, E. (1983).** The importance of carrion breeding in the maintenance of the Australian sheep blowfly *Lucilia cuprina* (Wiedemann) in low rainfall areas of Western Australia. **In:** The Proceedings of the Second National Symposium *Sheep Blowfly and Flystrike in Sheep*. Dept. Agriculture N.S.W.

- Morley, F.H.W., Donald, A.D., Donnelly, J.R., Axelsen, A. and Waller, P.J. (1976). Blowfly strike in the breech region of sheep in relation to helminth infection. *Aust. Vet. J.* **52**, 325-9.
- Murray, M.D. (1980). Blowfly strike in sheep in southern Australia. 3. Victoria. *Agric. Rec.* **7**, 54-8.
- Newman, L.J. and Clark, J. (1926). Trapping blowflies. *J. West. Aust. Dept. Agric.* **3**, 382-91.
- Nicholson, A.J. (1934). The influence of temperature on the activity of sheep blowflies. *Bull. Entomol. Res.* **25**, 85-99.
- Nicholson, A.J. (1950). Competition for food amongst *Luciliacuprina* larvae. *Int. Congr. Entomol. Proc. (Stockholm)*. **8**, 277-28.
- Norris, K.R. (1959). The ecology of sheep blowflies in Australia. *Monogr. Biol.* **8**, 514-44.
- Norris, K.R. (1965). The bionomics of blowflies. *Annu. Rev. Entomol.* **10**, 47-68.
- O'Donnell, I.J., Green, P.E., Connell, J.A. and Hopkins, P.A. (1981). Immunisation of sheep with larval antigens of *Lucilia cuprina*. *Aust. J. Biol. Sci.* **34**, 411-7.
- Ord, J. K. (1979). Time-series and spatial patterns in ecology. **In:** Cormack, R. M. and Ord, J. K. (eds.) *Spatial and Temporal Analysis in Ecology* Int. Co-op. Publ.

House. Maryland.

- Orton, C. J. and Shipp, E. (1983). Comparative laboratory testing of *Lucilia cuprina* oviposition supressants. **In:** The Proceedings of the Second National Symposium *Sheep Blowfly and Flystrike in Sheep*. Dept. Agriculture N.S.W.
- O'Sullivan, B. M., Perkins, I., Vokes, L., Stuter, G. and Hopkins, P. S. (1983). The ecology of *Lucilia cuprina* (Wiedemann) in western Queensland. **In:** The Proceedings of the Second National Symposium *Sheep Blowfly and Flystrike in Sheep*. Dept. Agriculture N.S.W.
- Payne, J.A. (1965). A summer carrion study of the baby pig (*Sus scrofa*). *Ecology* **46**, 592-602.
- Putman, R.J. (1977). Dynamics of the blowfly, *Calliphora erythrocephala*, within carrion. *J. Anim. Ecol.* **46**, 853-66.
- Putman, R.J. (1978). The role of carrion-frequenting arthropods in the decay process. *Ecol. Entomol.* **3**, 133-9.
- Reid, R.N.D. and Jones, A.L. (1976). The effectiveness of mulesing in flystrike control in Corriedale and crossbred sheep in Tasmania. *Proc. Aust. Soc. Anim. Prod.* **11**, 185-8.
- Roff, D. (1977). Dispersal in Dipterans : Its costs and consequences. *J. Anim. Ecol.* **46**, 443-56.

- Roff, D. (1981). On being the right size. *Am. Nat.* 118, 405-22.
- Ryan, A.F. (1954). The sheep blowfly problem in Tasmania. *Aust. Vet. J.* 30, 109-13.
- Salt, G. (1932). The natural control of the sheep blowfly *Lucilia sericata* Meigen. *Bull. Entomol. Res.* 23, 235-45.
- Sands, P. and Hughes, R.D. (1977). Mathematical model of the survival rates of female bushflies (*Musca vetustissima* Walker) (Diptera : Calliphoridae) as inferred from field populations. *Bull. Entomol. Res.* 67, 675-83.
- Smith, P.H., Dallwitz, R., Wardhaugh, K.G., Vogt, W.G. and Woodburn, T.L. (1981). Timing of larval exodus from sheep and carrion in the Sheep Blowfly *Lucilia cuprina*. *Entomol. Exp. Appl.* 30, 157-62.
- Sokal, R.R. and Oden, N.L. (1978a). Spatial autocorrelation in biology 1. Methodology. *Biol. J. Linn. Soc.* 10, 199-228.
- Sokal, R.R. and Oden, N.L. (1978b). Spatial autocorrelation in biology 2. Some biological implication and four applications of evolutionary and ecological interest. *Biol. J. Linn. Soc.* 10, 229-49.
- Sullivan, R.L. and Sokal, R.R. (1963). The effects of larval density on several strains of the house fly. *Ecology* 44, 120-30.

- Ulyett, G.C. (1950). Competition for food and allied phenomena in sheep blowfly populations. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 234, 77-175.
- Unwin, D.M. and Corbet, S.A. (1984). Wingbeat frequency, temperature and body size in bees and flies. *Physiol. Entomol.* 9, 115-21.
- Vogt, W.G. and Havenstein, D.E. (1974). A standardised bait trap for blowfly studies. *J. Aust. Entomol. Soc.* 13, 249-53.
- Vogt, W.G. and Woodburn, T.L. (1979). Ecology, distribution and importance of sheep myiasis flies in Australia. In: The Proceedings of the First National Symposium *Sheep Blowfly and Flystrike in Sheep*. Dept. Agriculture N.S.W.
- Vogt, W.G. and Woodburn, T.L. (1982). Dispersal of post-feeding larvae of *Lucilia cuprina* (Wiedemann) (Diptera:Calliphoridae). *J. Aust. Entomol. Soc.* 21, 289-91.
- Vogt, W.G., Woodburn, T.L. and Tyndale-Biscoe, M. (1974). A method of age determination in *Lucilia cuprina* (Wied.) (Dipter : Calliphoridae) using cyclic changes in the female reproductive system. *Bull. Entomol. Res.* 64, 365-70.
- Wardhaugh, K.G. and Dallwitz, R. (1983). Covert flystrike. In: The Proceedings of the Second National Symposium *Sheep Blowfly and Flystrike in Sheep*. Dept. Agriculture N.S.W.
- Wardhaugh, K.G., Read, P. and Neave, M. (1983b). A sticky trap for studying the spatial distribution of the Australian sheep blowfly *Lucilia cuprina* (Wiedemann) In:

The Proceedings of the Second National Symposium *Sheep Blowfly and Flystrike in Sheep*. Dept. Agriculture N.S.W.

Wardhaugh, K.G., Smith, P.H. and Crompton, G.W. (1983a). A comparison of ground and aerial release methods for the genetic control of *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae). *Gen. Appl. Entomol.* 15, 37-46.

Wardle, R.A. (1930). Significant variables in the blowfly environment. *Ann. Appl. Biol.* 17, 554-74.

Waterhouse, D.F. (1947). The relative importance of live sheep and of carrion as breeding grounds for the Australian sheep blowfly *Lucilia cuprina*. *Aust. CSIRO Bull.* 217.

Waterhouse, D.F. and Paramonov, S.J. (1950). The status of the two species of *Lucilia* (Diptera : Calliphoridae) attacking sheep in Australia. *Aust. J. Sci. Res.* 3, 310-36.

Watts, J.E., Merritt, G.C. and Goodrich, B.S. (1981). The oviposition response of the Australian sheep blowfly *Lucilia cuprina* to fleece-rot odours. *Aust. Vet. J.* 57, 450-4.

Watts, J.E., Muller, M.J., Dyce, A.L. and Norris, K.R. (1976). The species of flies reared from struck sheep in south-eastern Australia. *Aust. Vet. J.* 52, 488-9.

Watts, J.E., Murray, M.D. and Graham, N.P.H. (1979). The blowfly strike problem of sheep in New South Wales. *Aust. Vet. J.* 55, 325-34.

Webber, L.G. (1955). The relationship between larval and adult size of the Australian

sheep blowfly *Lucilia cuprina* (Wied.). *Aust. J. Zool.* 3, 346-53.

Whitten, M.J., Foster, G.G., Vogt, W.G., Kitching, R.L., Woodburn, T.L. and Konovalov, C. (1977). Current status of genetic control of the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann) (Diptera : Calliphoridae). *Int. Cong. Entomol. Proc. (Washington)*. 15 129-39.

Williams, H. (1981). *Aspects of the ecology of the major Tasmanian necrophagous flies (Diptera : Calliphoridae)* Honours Thesis, University of Tasmania.

Williams, H. and Richardson, A.M.M. (1983). Life history responses to larval food shortages of four species of necrophagous flies (Diptera : Calliphoridae). *Aust. J. Ecol.* 8, 257-63.

Williams, H. and Richardson, A.M.M. (1984). Growth energetics in relation to temperature for larvae of four species of necrophagous flies (Diptera : Calliphoridae). *Aust. J. Ecol.* 9, 141-52.

Woodburn, T.L. and Vogt, W.G. (1982). Attractiveness of merino sheep before and after death to adults of *Lucilia cuprina* (Wiedmann) (Diptera : Calliphoridae). *J. Aust. Entomol. Soc.* 21, 131-4.

Woodburn, T.L., Vogt, W.G. and Kitching, R.L. (1978). Estimation of age of females in field populations of *Lucilia cuprina* (Wiedmann) (Diptera : Calliphoridae) using ambient temperatures and solar radiation. *Bull. Entomol. Res.* 68, 251-61.

Zumpt, F. (1965). *Myiasis in Man and Animals in the Old World.* Butterworths, London.

APPENDIX 1

(a) SIMULATION MODEL OF SIZE EFFECTS ON POTENTIAL EGG PRODUCTION
WITH NO DEVELOPMENTAL DELAYS

```

REM MODEL OF EGG PRODUCTION FOR L.CUPRINA OVER THREE GONADOTROPHIC CYCLES
REM ASSUMING A FIXED LARVAL RESOURCE, THE COMPETITIVE REGIME IS VARIED TO
REM GIVE DIFFERENT SIZED ADULTS. THE EFFECTS OF THE DIFFERENT LARVAL AND
REM ADULT SURVIVAL RATES (BY SIZE) ON THE NUMBER OF ADULTS EMERGING ON
REM EGG PRODUCTION ARE MODELLED USING THE REGRESSION EQUATIONS DERIVED
REM IN CHAPTER 4, AND THE LITERATURE (REFERENCED IN THE PROGRAM)
REM TEMPERATURES ARE SET TO 35°C (LARVAL) AND 20°C (ADULT)

```

```

REM THE ARRAY OUT(X,Y) STORES THE VALUES FOR EGG PRODUCTION (X=1),
REM NUMBER OF FEMALES PRODUCED (X=2), NUMBER OF BATCHES (X=3),
REM EGGS PER ADULT (X=4), AND EGGS PER DAY (X=5)
DIM OUT(5,20),OPTCY(3):DEFDBL L

```

```

REM READ IN DAYDEGREE TABLE FOR 1ST,2ND,3RD CYCLE FROM VOGT ET AL(1974)
REM STORE THE VALUES IN THE ARRAY OPTCY(*)

```

```

DATA 61,96,131
FOR I =1 TO 3
  READ OPTCY(I)
NEXT I

```

```

REM NOW START CALCULATIONS FROM THE SMALLEST ADULT SIZE

```

```

Y=0
FOR TL = 2.65 TO 4.55 STEP .1
  Y=Y+1:REM Y IS A COUNTER FOR THE OUTPUT TABLES
  REM CALCULATE THE EXPECTED BATCH SIZE
  EXPEGG=23.364*(TL^1.645)

```

```

REM CALCULATE INITIAL NUMBER OF LARVAE ON 10G SUBSTRATE
REM TO GIVE FEMALES OF SET TL AT GIVEN TEMPERATURE

```

```

REM SET LARVAL TEMPERATURE

```

TEMP=35

CONS=((TL-2.4058-(.0053*TEMP))/ .0296)/1000

REM CONS GIVES GRAMS DRY WEIGHT REQUIRED TO PRODUCE ADULT

REM (FEMALE) OF TL AND 10G OF MRM IS EQUIVALENT OF 1.42G DW.

NLARV=1.42/CONS

REM NLARV GIVES NUMBER OF LARVAE ON 10 G SUSTRATE IE.1.42 G DW.

REM CALCULATE COMPETITIVE REGIME AND EXPECTED EGG-ADULT S(X)

LPERMG=10/NLARV

REM CALCULATE LARVAL SURVIVORSHIP FROM REGRESSION

SXLARV=(.282*LOG(LPERMG))+1.427

REM SURVIVAL CANNOT EXCEED 1

IF SXLARV > 1 THEN SXLARV=1

REM CALCULATE SEX RATIO AND NUMBER OF FEMALES EXPECTED

SEXRAT=-1.9241+(.7562*TL)+(.0278*TEMP)

NMAL=(SXLARV*NLARV)/(SEXRAT+1)

NFEM=(SXLARV*NLARV)-NMAL

REM STORE THE VALUE FOR OUTPUT

OUT(2,Y)=NFEM

REM CALCULATE EGG PRODUCTION FOR 2 CYCLES, AND CONFIGURE SURVIVOR

REM CURVE SO THAT THERE ARE NONE LEFT AT END OF CYCLE 2.

REM FIRST CALCULATE DEVELOPMENT DIFFERENTIAL FOR SIZE USING

REM DURATION OF PHARATE STAGE FOR TL=3.8 AS STANDARD (SPHAR)

RPHAR=-.3673+(.0202*TEMP)+(.0283*TL)

REM CONVERT THIS TO A RATE

RPHAR=1/RPHAR

SPHAR=-.25976+(.0202*TEMP)

REM CONVERT THIS TO A RATE

```
SPHAR=1/SPHAR
```

```
REM NOW CALCULATE THE DIFFERENCE
```

```
DDIF=(RPHAR/SPHAR)
```

```
REM USING THE DEVELOPMENT SCHEDULE IN OPTCY(*) ADJUST FOR
```

```
REM SIZE WITH DDIF AND CALCULATE NUMBER OF FEMALE SURVIVORS
```

```
REM AND THEIR EGG PRODUCTION
```

```
FOR I = 1 TO 3
```

```
  CYC(I)=OPTCY(I)*DDIF
```

```
NEXT I
```

```
REM NOW CALCULATE NO. FEMALES EXPECTED TO SURVIVE TO THESE AGES
```

```
REM SET ADULT TEMPERATURE TO 20°C
```

```
TEMP=20
```

```
REM FIRST THE LAB SURVIVAL MUST BE CORRECTED TO FIELD SURVIVAL
```

```
REM CALCULATE MIDPOINT IE DAY ON WHICH SURVIVORS=50%.
```

```
CDAY50=(CYC(3)/(TEMP-11.3))/2
```

```
REM SOLVE LOGIT EQUATION FOR 50% MORTALITY
```

```
LDAY50=(8.1285-(.2362*TEMP)+(.1559*TL))/ .0761
```

```
REM NOW CALCULATE A CONVERSION FACTOR SO THAT THE LAB LOGIT
```

```
REM REGRESSION CAN BE FORCED TO FOLLOW FIELD SURVIVAL
```

```
CONVERT=LDAY50/CDAY50
```

```
FOR CYCLE = 1 TO 3
```

```
  REM CALCULATE AGE IN DAYS (USING A DEVELOPMENTAL ZERO
```

```
  REM OF 11.3°C)
```

```
    DAYS=CYC(CYCLE)/(TEMP-11.3)
```

```
  REM CALCULATE LOGIT AND TRANSFORM TO SURVIVORS
```

```
    LOGIT=-8.1285+(.0761*DAYS*CONVERT)+(.2362*TEMP)-(.1559*TL)
```

```

SURV=1-( (EXP (LOGIT)) / (EXP (LOGIT)+1) )
SURV=SURV*NFEM

```

NOTE: This is where the delay routine [in (b) below is added]

```

REM ACCUMULATE THE NUMBER OF BATCHES PRODUCED
OUT(3,Y)=SURV+OUT(3,Y)

```

```

REM CALCULATE EXPECTED EGG PRODUCTION OF SURVIVORS AND SUM
REM OVER PRECEEDING CYCLES OF EGG PRODUCTION
EGGS=SURV*EXPEGG+EGGS

```

```

NEXT CYCLE

```

```

REM STORE THE ACCUMULATED EGG PRODUCTION EGGS PER ADULT AND EGGS
REM PER DAY
OUT(1,Y)=EGGS
OUT(4,Y)=EGGS/OUT(2,Y)
OUT(5,Y)=EGGS/(CDAY50*2)

```

```

REM INITIALISE THE ACCUMULATOR EGGS FOR ANOTHER RUN THRU THE LOOP
EGGS=0!

```

```

NEXT TL

```

```

REM NOW WRITE THE OUTPUT TO LINEPRINTER
10 BEEP:INPUT"IS THE PRINTER READY";A$
IF A$ <> "Y" THEN GOTO 10

```

```

REM SET UP THE OUTPUT TABLE
OPEN "CLIP:" FOR OUTPUT AS #1
LPRINT ;"TL";TAB(10);"TOT EGG PROD. "; "FEMALES PROD. "; "TOT BATCHES
";"EGGS/ADULT "; "EGGS/DAY "
WRITE #1, "TL","EGG PROD","FEMS PROD","BATCHES","EGGS/ADULT","EGGS/DAY"
FOR I = 1 TO 85:LPRINT "_";:NEXT I:LPRINT

```

```
REM PRINT OUTPUT
```

```
FOR Y = 1 TO 20
```

```
  TL=2.55 +(Y*.1):LPRINT USING "#.##";TL;
```

```
  WRITE #1,TL,OUT(1,Y),OUT(2,Y),OUT(3,Y),OUT(4,Y),OUT(5,Y)
```

```
    FOR X = 1 TO 5
```

```
      J=(X-1)*15+10
```

```
      LPRINT ;TAB(J);USING "#####.##";OUT(X,Y);
```

```
    NEXT X:LPRINT
```

```
  NEXT Y:LPRINT
```

```
CLOSE #1
```

```
STOP
```

(b) ALGORITHM FOR ADDING DEVELOPMENTAL DELAYS TO THE
SIMULATION

```
REM CALCULATE DELAYS FROM THE REGRESSION AND ASSUME THAT  
REM DURATION IS FOR AT LEAST ONE CYCLE. AS THERE ARE ONLY  
REM TWO EGG CYCLES IN THIS MODEL, THIS EFFECT CAN BE APPROXIMATED  
REM BY SIMPLY SUMMING THE NUMBER OF DELAYED FLIES
```

```
  NDELAY=(48.964*TL - 128.616)/100
```

```
REM CALCULATE THE NUMBER OF REPRODUCTIVE SURVIVORS
```

```
  SURV = SURV-(SURV*NDELAY)
```

```
  IF CYCLE = 2 THEN SURV = SURV -(SURV*NDELAY)
```

APPENDIX 2**RELATED PUBLICATIONS**

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McQuillan, P., Jones, A.L. and Williams, H. (1983). Recent studies on sheep blowflies (Diptera: Calliphoridae) in Tasmania. In: The proceedings of the Second National Symposium Sheep Blowfly and Flystrike in Sheep. Dept. Agriculture N.S.W.

Life history responses to larval food shortages in four species of necrophagous flies (Diptera : Calliphoridae)

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Abstract

The effects of artificially reduced amounts of larval food on various life history parameters of *Lucilia cuprina*, *Calliphora stygia*, *C. vicina*, and *C. hilli* were measured to assess the likely reaction of these blowflies to competition in carrion. With increasing food shortage the puparia were reduced by up to 12% of the weight attained under conditions in which food was unlimited. The size of eggs laid by adults which had been subject to food deprivation as larvae was unchanged, but all species showed a reduction in the number of ovarioles. An index of mass-specific reproductive investment varied considerably between the species, and the relationships between this index and the preferred habitats and dispersal strategies of the species are discussed.

Introduction

The larvae of flies which breed in carrion regularly suffer both inter- and intra-specific competition as an inevitable consequence of the finite nature of the food resource (Ulyett 1950). This competition may lead to the extinction of a species in one carrion unit. Hanski (1977) suggests that while this is not an event critical to the persistence of regional fly populations, success or failure in migration from one carrion unit to another is of overwhelming importance.

Although competition may be strong enough to limit the growth of larvae, this will not always result in extinction, because although mortality rates rise predictably with increasing competition (e.g. in

Lucilia cuprina: Readshaw & Cuff 1980), its effect is reduced by the ability of most carrion species to produce fractional individuals, i.e. small but viable adults. The fecundity of these fractional adults is reduced with their size, but they retain the ability to emigrate from the carcass and colonize another.

In southern Tasmania, the major species making up the necrophagous fly guild are *Lucilia cuprina*, *Calliphora vicina*, *C. stygia* and *C. hilli*. Since all these species are to some degree necrophagous, comparisons between them seem valid. It is likely that *Lucilia cuprina* bred originally on carrion, but now seems to breed primarily through myiasis (Mackerras 1936; Waterhouse 1947). This is in reality only a slight extension of normal blowfly behaviour (Norris 1959). This change in habit seems likely to have occurred within the last century (Waterhouse & Paramonov 1950), perhaps as a result of competition from other species utilizing carrion.

Williams and Richardson (in prep.) have shown that *Chrysomya rufifacies* is not present in southern Tasmania and that there are no calliphorids capable of outcompeting *L. cuprina* at temperatures greater than 15°C, thus there is at least the possibility that *L. cuprina* could be successful in carrion in Tasmania. This is in contrast to the situation on the mainland of Australia where *L. cuprina*'s success in carrion is suppressed by (i) predation by *Chrysomya rufifacies*, (ii) the generation of temperatures above its tolerance range by *Ch. rufifacies* and (iii) competition from other Calliphorids (Mackerras 1936).

Collins (1980) has described an approach by which inferences can be drawn about the contribution of various life history features to overall fitness from phenotypic changes in those features caused by naturally occurring stresses (such as the shortage of larval food). He suggested that the degree to which a life history feature deteriorates in

response to a realistically applied, naturally occurring stress, should be an inverse measure of the importance of that feature to fitness.

This paper examines the effects of reduced larval food on a guild of necrophagous flies, with a view to establishing (1) the importance of food shortages as a variable in their lives, and (2) whether differences in their responses to food shortages are contributing to the separation between their niches.

Methods

Eggs of *Lucilia cuprina*, *Calliphora stygia* and *Calliphora vicina* were obtained from breeding cultures kept at the university for at least two generations. The sheathed larvae of the ovoviviparous *Calliphora hilli* were obtained by dissection from wild gravid females.

Larvae were cultured on 80 g of beef liver placed on a 90 mm Petri dish. The dish was placed on top of vermiculite in a larger container. The vermiculite had been stored at 25°C and a relative humidity of 80±10%, so that it was moist when used, in order to prevent desiccation of the pupae.

Crowded, pure cultures of the larvae were raised at 15°C and a density of approximately 100 larvae/10 g liver (*Calliphora* spp.) at 25°C, and approximately 200 larvae/10 g liver (*L. cuprina*). Uncrowded control cultures were raised at the same temperatures with densities of 25 larvae/10 g liver for the *Calliphora* species and 50 larvae/10 g liver for *L. cuprina*.

After hatching, larvae were removed every 4 h from the crowded cultures (excluding an 8 h period at night). The sampling period allowed approximately 25 samplings for *L. cuprina* and *C. hilli* and 50 samplings for *C. stygia* and *C. vicina* before the feeding stage finished. These samples were placed in individual glass vials filled with vermiculite and kept under the same temperatures and humidities as described above. Since Ferrar (1979) noted that

disturbance in the early pupal stages could be fatal, the pupae were not handled until 48 h after formation, when they were extracted and their lengths measured.

These samples were then divided into two groups. In the first group pupae of known length were dried for 24 h at 60°C in a vacuum oven and then weighed on a Sartorius 4125 microbalance. In the second group, individual pupae of known lengths were placed in vermiculite-filled glass vials and stored, at the same constant temperatures as used for the larval cultures, until emergence. At emergence the male flies were discarded and the females subdivided into another two groups. From the first, which did not include *L. cuprina*, the ovaries were dissected, stained (Vogt *et al.* 1974) and the number of ovarioles counted. Data was not collected for *L. cuprina*, since a relationship between pupal live weight and number of ovarioles is available (Webber 1955). In order to use this, a relationship was established between pupal dry weight and pupal live weight for pupae approximately 12 h before emergence. Webber's original allometric relationship was then recalculated to give pupal dry weight and ovariole number.

Females from the second group (11 of *C. stygia* and *C. vicina*, and eight of *L. cuprina*) were isolated with two males and fed 3 M sucrose solution and liver exudate for the first four days after emergence, after which time the liver exudate was exchanged for pieces of beef liver (approximately 20 g). The liver was replaced daily, and checked for eggs every 12 h. If eggs were present they were removed from the liver as a solid cluster and teased apart to separate at least 20 eggs. The eggs were dried for 24 h at 60°C in a vacuum oven and weighed on the microbalance. *C. hilli* could not be included in this procedure as it was not possible to rear females successfully while maintaining normal ovarian function. The controls were left undisturbed until about 48 h after pupae had formed. Samples of approximately 25 were then removed and their length recorded.

TABLE 1 Minimum pupal lengths and the magnitude of their reduction from mean optimal size

Species	Minimum pupal length (mm)	Reduction as % of mean optimal length weight		Mean optimal length (mm)
<i>L. cuprina</i>	4.50	57.7	21.0	7.80
<i>C. hilli</i>	6.30	67.0	28.6	9.40
<i>C. stygia</i>	7.00	57.8	24.8	12.10
<i>C. vicina</i>	5.25	48.2	12.3	10.90

Results

The minimum pupal sizes found in the four species are shown in Table 1 and expressed as percentages of the mean size attained under control conditions, i.e. those obtained from larvae which had fed to repletion and left the substrate in the normal course of their development.

Although reduction in pupal length in all species reduces the number of eggs laid in a clutch by the ensuing adults (Fig. 1), it does not affect the weight of eggs produced by the adults of *L. cuprina*, *C. stygia* and *C. vicina* (Table 2). The results of non-linear regression of pupal length against number of ovarioles are given in Table 3, and in all cases the regressions are significant. Analysis of the linear regressions describing the relationship between pupal length and the size of the ensuing eggs showed that in all cases the slopes of the regressions do not differ significantly from zero (Table 2) and thus egg size is constant and independent of pupal size.

TABLE 2 Regression constants and coefficients of determination (r^2) for the regression of egg weight (y) against pupal length (x) in the form $y = a + bx$ (Probability of slope being equal to 0 is shown)

Species	a	b	r^2	$P(b=0)$
<i>L. cuprina</i>	0.029	- 0.001	0.007	$P>0.05$
<i>C. stygia</i>	0.064	- 0.001	0.034	$P>0.05$
<i>C. vicina</i>	0.045	- 0.0004	0.031	$P>0.05$

TABLE 3 Regression constants for the regression (by transformation to linear) of number of ovarioles (y) against pupal length (x) in the form $y = ax^b$

Species	Regression constants		Regression statistics		
	a	b	n	r^2	P
<i>L. cuprina</i>	2.93	2.38	*		
<i>C. hilli</i>	0.03	3.64	27	0.94	$P<0.0025$
<i>C. stygia</i>	0.02	3.82	11	0.95	$P<0.0025$
<i>C. vicina</i>	1.14	2.19	32	0.93	$P<0.0025$

*Adapted from Webber (1955)

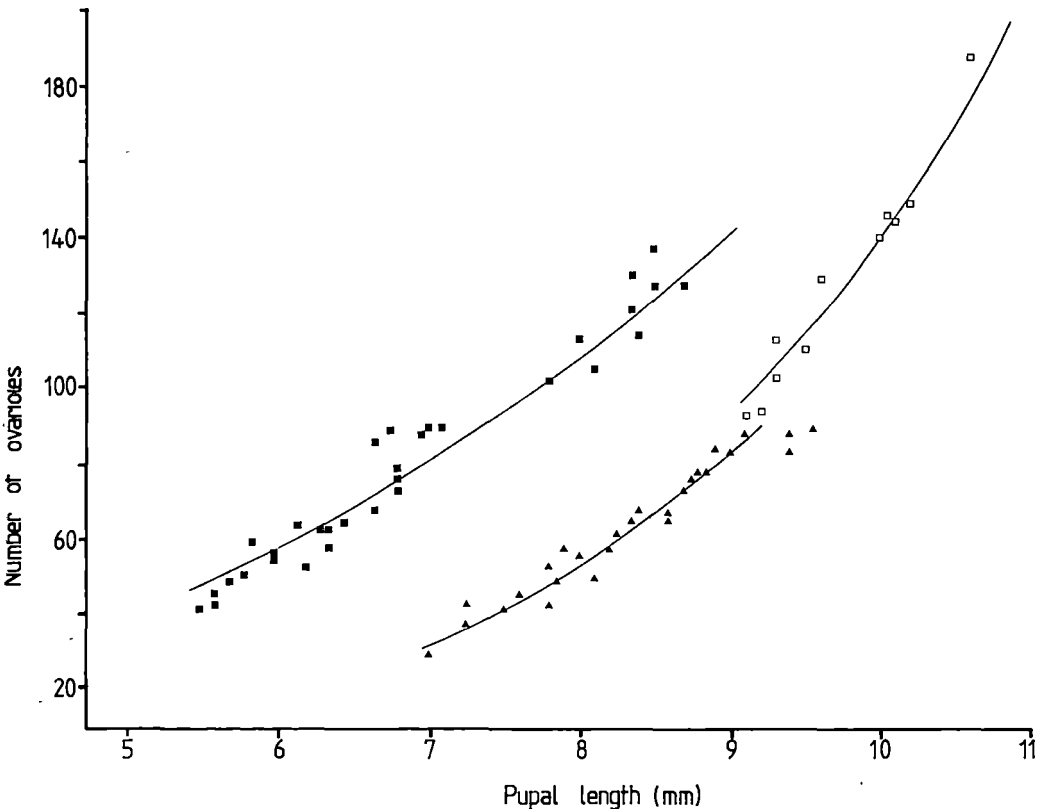


FIG 1 The relationship between pupal length and number of ovarioles for *C. vicina* ■, *C. stygia* □ and *C. hilli* ▲

Non-linear regression analysis was used to establish relationships between (1) pupal length and pupal dry weight and (2) pupal length and the number of ovarioles produced in the emerged female. Since pupal length is common to both these relationships, the relationship between pupal dry weight and number of ovarioles could be derived as an index of mass-specific reproductive investment, R_1 , (Collins 1980) which is defined as $R_1 = Ov_n/P_w$ where Ov_n is the number of ovarioles for a female emerging from a pupae of known dry weight P_w .

The index expresses the relationship between the reproductive effort (as ovariole number is an indirect measure of the number of eggs produced in one ovarian cycle) and the original pupal mass of the fly.

Table 4 gives the results of the regression of pupal dry weight against pupal length (Fig. 2) which permits the conversion of pupal length to the dry weights used in the calculation of the mass specific reproductive index.

The mass specific reproductive investment index, R_1 , is plotted against pupal weight in Fig. 3. The results show three responses of R_1 to increasing pupal weight: (1) a decrease in R_1 , that is a diversion of a greater proportion of the available energy to reproductive effort in the smaller forms. This is seen in *L. cuprina* and to a much less marked extent in *C. vicina*; (2) an increase in R_1 , or an increase in

TABLE 4 Regression constants for pupal dry weight (y) against pupal length (x) in the form $y = ax^b$, transformation to linear regression used

Species	Regression constants		Regression statistics		
	a	b	n	r^2	P
<i>L. cuprina</i>	0.03	3.14	35	0.96	$P < 0.0025$
<i>C. hilli</i>	0.02	3.13	31	0.94	$P < 0.0025$
<i>C. stygia</i>	0.06	2.55	27	0.77	$P < 0.0025$
<i>C. vicina</i>	0.04	2.86	33	0.94	$P < 0.0025$

TABLE 5 The range and magnitude of R_1 values from Fig. 4

	Range of R_1 values	Change in R_1 from minimum to maximum pupal weight
<i>L. cuprina</i>	22.0–33.0	–11.0
<i>C. hilli</i>	4.0–5.0	+1.0
<i>C. stygia</i>	4.0–8.0	+4.0
<i>C. vicina</i>	6.3–9.5	–3.2

investment in the larger forms (*C. stygia*); and (3) a small and probably insignificant increase in R_1 in *C. hilli* suggesting that R_1 remains more or less constant over all sizes.

The range of R_1 seen in each species is given in Table 5. The largest changes are seen in *L. cuprina*

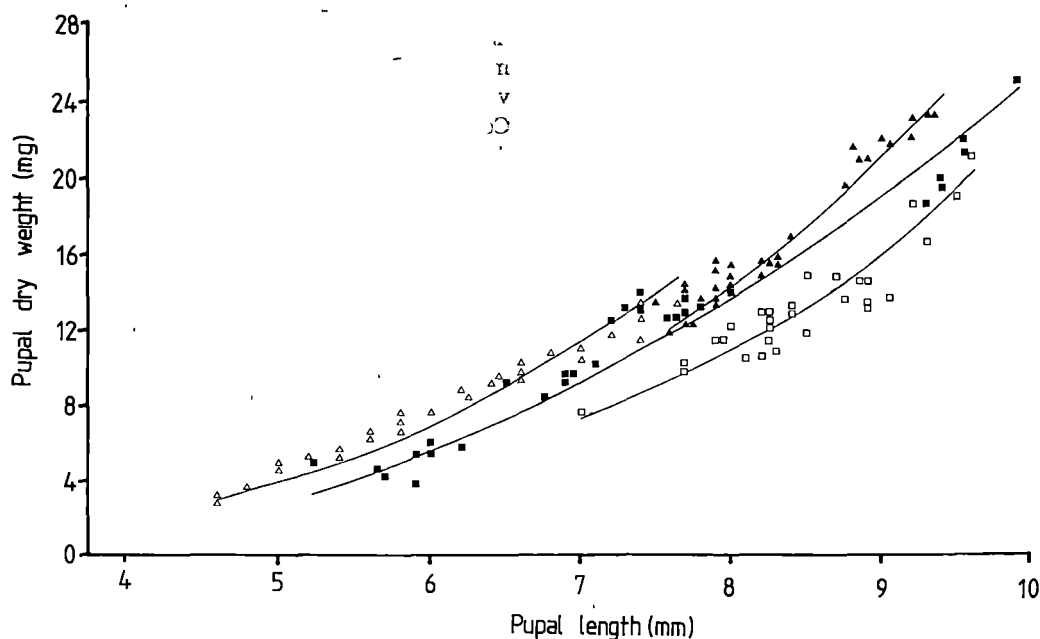


FIG. 2 The relationship between pupal length and pupal dry weight for *C. vicina* ■, *C. stygia*, □ and *C. hilli* ▲ and *L. cuprina* △.

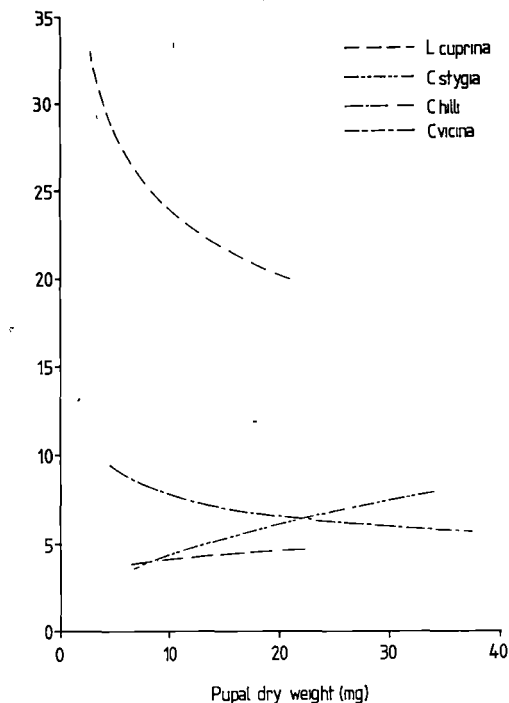


FIG 3 The relationship between the index of mass specific reproductive investment (R_1) and the dry weight of female pupae

and *C. stygia*, while those of *C. hulli* and *C. vicina* are probably insignificant. The highest reproductive load found in the *Calliphora* species (i.e. $R_1 = 9.5$ in *C. vicina*) is less than half that of the lowest load in *L. cuprina* ($R_1 = 22$). This suggests that allocation of energy to other functions such as dispersal is less important than reproductive effort in *L. cuprina* and conversely more important in the *Calliphora* species.

Discussion

Levot *et al.* (1979) determined the minimum sizes of larvae necessary for pupation for the common blowflies found in south-eastern Australia using larvae raised in uncrowded conditions. They observed that two species common to this study, *L. cuprina* and *C. stygia*, formed pupae at a minimum of 60% and 73% of the normal size, respectively, significantly larger than those recorded in this study. However in another study, in which crowded larval cultures were used (Webber 1955), a reduction in pupal size for *L. cuprina* comparable to ours was recorded (22%, as compared with 21% in this

study). It may be that there is a density-dependent mechanism inducing larvae to pupate at sub-optimal sizes, but such an explanation must take into account the behaviour of the feeding larvae, which form discrete feeding clusters whatever the conditions of crowding on the food source may be. Thus a density-dependent factor cannot be deduced simply from the spatial arrangement of the larvae, but rather by relating larval numbers to the overall availability of the food source. Ulyett (1950) has shown that with increasing shortage of food the length of the feeding stage remains constant while the growth increments are reduced. As larvae do not leave and pupate immediately on encountering food shortages, competition for feeding sites within the feeding cluster would be increased and feeding would be discontinuous, or at least inhibited, resulting in a reduction in the volume of food ingested.

The lack of any significant relationship between pupal size and the size of eggs produced suggests that egg size has a critical minimum close to the normal size, which may represent the amount of energy required to initiate larval development without adversely affecting the competitive ability of the larvae.

Pre-adult mortality in calliphorids can be very high (up to 80% in *C. vicina*; Putman 1977), with the majority of the deaths occurring between the end of feeding and the emergence of the adults. Ulyett (1950) has shown that even though food shortage may force pupation at sizes of only 60–70% of the mean, blowfly larvae do not lengthen their development time in order to obtain more food. As Collins (1980) points out, this would only increase their mortality in view of the high pre-reproductive mortality rates. A shortened development time only carries the minor penalty of smaller adult size.

Extending this argument, the consequences of smaller adult size, such as increased energy costs for flight (Roff 1977), and decreased fecundity, must be of less importance to the fitness of adult flies than the increased risk of mortality in the larval or pupal stage. This conclusion was also reached indirectly by Hanski (1977), who considered that extinction is not a significant variable when considering carrion units, but rather that success or failure in dispersal from the carcass is of paramount importance. This is more likely to be achieved by the production of many small flies than a few large ones. This variation will have no effect on the fitness of the members of the next generation, since egg size remains constant, ensuring that the resources available to

individuals of the next generation are constant, whatever the size of the adult that laid the eggs.

Experiments with *Drosophila melanogaster* show that energy expended in flight and reproductive effort are negatively correlated (Roff 1977). This is to be expected if the two functions are the major pathways for energy in adults as (1) energy allocated to one will reduce the finite energy reserve of the fly and thus the energy available to the other, and (2) energy allocated to reproduction will, by increasing the weight of fly in terms of egg tissue, require more energy in maintaining the flies ability to fly, and hence reduce flight length. With such a compromise there are three options available to a species which has the potential to produce small females. These are: (1) for the relative weight of a clutch produced by a female to remain the same (as in *C. hulli*) and thus allow the ratio of energy allocated to flight and egg production to remain the same over the range of adult sizes. (In this case the dispersive ability would be proportional to adult size alone); (2) for the clutch weight to decrease with decreasing adult size (as in *C. stygia*) leading to a higher allocation of energy to the dispersal of smaller forms, and so increasing their chances of finding carrion, but decreasing the number of eggs to deposit on that carrion; or (3) for the relative weight of the clutch to increase with decreasing adult size (as in *L. cuprina* and *C. vicina*), which would allow less energy to be allocated to flight. Thus the flies' chances of finding carrion would be diminished but the potential number of eggs deposited would remain the same.

Roff (1977) stated that energy consumption during flight would be inversely related to body size. From the present study it can be seen that at *L. cuprina*'s largest size its commitment to R_1 is approximately four times that of *Calliphora* species of similar sizes. Thus *L. cuprina*'s mobility should be reduced by a proportional amount.

Information is available in the literature on the dispersive ability of *Lucilia cuprina* and *C. stygia*. *Calliphora stygia* is known to have a stronger dispersive phase than *L. cuprina* (Norris 1965), and Kitching (1981) refers to *L. cuprina* as a locally sedentary form. This difference in mobility can be related to the spatial and temporal distribution of the preferred habitats of the flies (i.e. carrion for *C. stygia* and live sheep for *L. cuprina*). For instance, carrion is widely and unpredictably dispersed, and thus it requires strong and active searching for *C. stygia* to find suitable oviposition sites. On the other hand, live sheep are clumped in mobs and these

mobs have predictable spatial and temporal distributions (McBride *et al.* 1967). Indeed the timing of exodus by larvae from sheep should tend to clump the pupating (and thus emerging flies) at camp sites regularly visited by sheep (Smith *et al.* 1981). This self-reinforcing association between *L. cuprina* and its resource should decrease the mobility required by the species to exploit it. The response of *L. cuprina* to reduced adult size, i.e. increasing the amount of energy allocated to reproduction and hence decreasing that allocated to other areas (primarily dispersal), may be interpreted as a form of bet-hedging with regard to the production of the next generation. That is, even allowing for the lowered mobility of the adult, the proportion of females finding oviposition sites will justify the reproductive load carried in terms of the potential success of their progeny.

All the *Calliphora* species studied here occupy a narrow range of R_1 values, but it may be misleading to make comparisons within the *Calliphora* species as the compounding of errors from the original allometric relationships may cloud the significance of the differences in the relationships seen in Fig. 3. It can be suggested, however, that the dedication of less energy to reproduction in the *Calliphora* species may be related to the dispersion of their resource and the consequent demands on the mobility of the species utilizing it.

Stearns (1977) has suggested that there are problems in assessing the reliability of conclusions drawn about life history strategies from life history traits. These stem from the disparity between laboratory measured mortality and that observed in natural populations. Laboratory derived estimates of total fecundity are misleading because the number of reproductive cycles which an iteroparous species can complete will obviously depend on the length of its life. In this study we have dealt with a reproductive measure (R_1) which only bears relation to one reproductive cycle. In this context the initial ovariole number of teneral females may be considered a measure of potential fecundity, and so is independent of mortality. To validate this classification of the life history strategies of blowflies, based on R_1 , for natural populations would require life table data based on field observations.

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References

- Collins N C. (1980) Development responses to food limitation as indicators of environmental conditions for *Ephydra cinerea* Jones (Diptera) *Ecology* **61**, 650–61.
- Ferrar P (1979) The immature stages of dung-breeding Muscoid flies in Australia, with notes on the species and keys to larvae and puparia *Aust. J. Zool. Suppl. Ser. No. 73*, 1–106.
- Hanski I (1977) An interpolation model of assimilation by larvae of the blowfly *Lucilia illustris* (Calliphoridae) in changing temperatures *Oikos* **28**, 187–95.
- Kitching R L (1981) The sheep blowfly a resource-limited specialist species. In: *The Ecology of Pests Some Australian Case Histories* (eds R L Kitching and R E Jones), pp 193–214. CSIRO, Melbourne.
- Levot G W, Brown K R & Shipp E (1979) Larval growth of some calliphorid and sarcophagid Diptera *Bull. ent. Res.* **69**, 469–75.
- Mackerras I M (1936) The sheep blowfly problem in Australia. Results of some recent investigations *CSIRO Aust. Pamphlet* No 66.
- McBride G, Arnold G W., Alexander G & Lynch J J (1967) Ecological aspects of the behaviour of domestic animals *Proc. ecol. Soc. Aust.* **2**, 133–65.
- Norris K R. (1965) The bionomics of blowflies. *Ann. Rev. Entomol.* **10**, 47–68.
- Putman R J. (1977) Dynamics of the blowfly *Calliphora vicina* within carrion *J. Anim. Ecol.* **46**, 853–66.
- Readshaw J L & Cuff W R (1980) A model of Nicholson's blowfly cycles and its relevance to predation theory *J. Anim. Ecol.* **49**, 1005–10.
- Roff D (1977) Dispersal in dipterans: its costs and consequences *J. Anim. Ecol.* **46**, 443–56.
- Smith, P H., Dallwitz R, Wardhaugh K. G., Vogt W. G. & Woodburn T L. (1981) Timing of larval exodus from sheep and carrion in the sheep blowfly *Lucilia cuprina*. *Ent. exp. & appl.* **30**, 151–62.
- Stearns S. C. (1977) The evolution of life history traits *Ann. Rev. Ecol. Syst.* **8**, 145–72.
- Ulyett G. C. (1950) Competition for food and allied phenomena in sheep blowfly populations. *Phil. Trans. R. Soc. Lond. Ser. B.* **234**, 77–175.
- Vogt W G., Woodburn T. L. & Tyndale-Biscoe M (1974) A method of age determination in *Lucilia cuprina* (Wied.) (Diptera, Calliphoridae) using cyclic changes in the female reproductive system *Bull. ent. Res.* **64**, 365–70.
- Waterhouse D F. (1947) The relative importance of live sheep and of carrion as breeding grounds for the sheep blowfly *Lucilia cuprina*. CSIRO (Aust.) Bull. No 217.
- Waterhouse D. F. & Paramonov S J. (1950) The status of the two species of *Lucilia* (Diptera, Calliphoridae) attacking sheep in Australia *Aust. J. Sci. Res. Ser. B.* **3**, 310–36.
- Webber L. G. (1955) The relationship between larval and adult size of the Australian sheep blowfly *Lucilia cuprina* (Wied.) *Aust. J. Zool.* **3**, 346–53.

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Growth energetics in relation to temperature for larvae of four species of necrophagous flies (Diptera: Calliphoridae)

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Abstract

The growth characteristics of the larvae of the major members of a necrophagous fly guild in Tasmania (*Lucilia cuprina*, *Calliphora stygia*, *Calliphora vicina* and *Calliphora hulli*) were measured to assess their competitive ability. The measurements were made at temperatures between 10 and 45°C, to cover the range of temperatures that would be encountered by larvae in carrion or myiasis under field conditions.

The characteristics measured were net production and respiration. The indices K_{2t} (instantaneous growth efficiency), K_{2c} (cumulated growth efficiency) and M_i (instantaneous cost of maintenance) were calculated. Generally K_{2c} and K_{2t} are highest and M_i lowest at 25°C for all the species. A sinusoidal response in K_{2c} , K_{2t} and M_i against temperature is seen for *L. cuprina*, *C. stygia* and *C. vicina*. This response is 'cold' adapted in the *Calliphora* species and 'warm' adapted in *L. cuprina*.

Egg size, egg caloric density and the energy content of the eggs are discussed in relation to the 'fitness' and reproductive strategies of the four species.

The thermal tolerance range of *L. cuprina* determined here suggests that carrion may provide a significant number of this fly particularly in areas where *Chrysomya* spp. do not occur, and in large carcasses where temperatures are elevated.

Introduction

The Calliphoridae are a large cosmopolitan family of flies with rather specialized life cycles and generally localized breeding sites. Many members of the sub-family Calliphorinae are necrophagous, a

habit facilitated by the rapid growth, high metabolic rate and resulting short feeding phase of their larvae (Roback 1951).

The success of the Calliphoridae can be seen in their dominance of carrion communities (Payne 1965; Putman 1978). The nature of this food resource often leads to intense competition between larvae. Ullyett (1950) suggested that the extent to which a species suffers from competition depends on its growth rate, and its ability to form viable pupae from small larvae. In an extension to this argument, Denno and Cothran (1976) suggested that reproductive strategies will affect the ability of larvae to compete. Their study showed that the advantage of ovoviviparity in the sarcophagids is the production of a small number of offspring, which avoid competition with oviparous species by having no embryonic delay, and are thus able to complete their feeding phase before the oviparous species over-utilize the resource.

Previous work in Australia has mainly been directed towards establishing whether carrion provides the source of a significant number of adult *Lucilia cuprina* (Wiedemann), because of concern over the involvement of this introduced blowfly in sheep strike. Mackerras (1936) and Waterhouse (1947) concluded that carrion was not a significant source of *L. cuprina*. Mackerras suggested that this was due to superior competition from *Calliphora* spp., and predation by larvae of *Chrysomya rufifacies*. In contrast, Waterhouse implicated the unfavourably high temperatures occurring in large carcasses as the reason for *L. cuprina*'s poor performance in carrion. This phenomenon was attributed to the metabolic activity of *Ch. rufifacies* and other native calliphorid larvae, elevating the carcass temperature above ambient temperature.

These conclusions about *L. cuprina* were reached on the mainland of Australia, but there is doubt about the presence of all the members of the south-eastern Australian blowfly guild in Tasmania. Ryan (1952), in a review of the Tasmanian blowfly fauna, did not record either *Chrysomya rufifacies*, *Ch. varipes* (Macquart) or *Calliphora augur* (Fabricius)

In a recent trapping program in northern Tasmania and Flinders Island, *Ch. rufifacies* and *Ch. varipes* were found in significant numbers, and *Calliphora augur* was found in low numbers (P. McQuillan pers. comm.). However, trapping by one of us (H.W) using standard 'West Australian' bait traps over two seasons in southern Tasmania has failed to detect these species. The major flies trapped were the ovoviviparous *Calliphora hilli* Patton, and the oviparous *C. vicina* Robineau-Desvoidy, *C. stygia* (Fabricius) and *Lucilia cuprina*. There is also the suggestion that the *Chrysomya* spp. are migratory, rather than having permanent local populations on mainland Tasmania. This is based on the late first occurrence of *Chrysomya* spp. in traps in northern Tasmania, compared to the temporal distribution seen in south-eastern Australia. Due to the absence of *Chrysomya* spp. it is suggested that the conclusions reached about *L. cuprina* on the Australian mainland might not apply in southern Tasmania.

The life cycle of calliphorids consists of an egg, three larval instars, a prepupa, a pupa and an adult. The larvae feed in the first two larval instars and the early third instar. Midway through the third instar, the larvae enter the wandering stage where they leave the food source and enter the surrounding substrate in search of pupation sites. A quiescent stage is entered at the end of this instar and is characterized by the contraction of the body and inactivity. The prepupal stage starts when quiescent larvae remain inactive even when disturbed, and is followed rapidly by the pupal stage.

The aim of this paper is to investigate the competitive abilities of the four blowflies commonly present in southern Tasmania. As inter-specific competition is only likely to be significant in the larval feeding phase when larvae compete for a common food source, this study is primarily concerned with the energetics of larval growth. However, for comparative purposes, the other stages are dealt with briefly.

Materials and methods

Cultures

Eggs of *L. cuprina*, *C. stygia* and *C. vicina* were obtained from breeding cultures kept at $20 \pm 2^\circ\text{C}$ at the university for 2–5 generations. The sheathed larvae of the ovoviviparous *C. hilli* were obtained by dissection from gravid females caught in bait traps. This method was used as no means of culturing the adults is known.

Monospecific larval cultures were set up at constant temperatures of 10, 15, 20, 25, 30, 35, 40 and 45°C (all $\pm 1^\circ\text{C}$) with relative humidities of 80–100%. The larvae were cultured on beef liver, (which was supplied *ad libitum*) placed on a 90 mm Petri dish. The dish was placed on top of vermiculite in a larger container. The vermiculite had been stored at 25°C and $80 \pm 10\%$ RH, so that it was moist when used, in order to prevent desiccation of the pupae.

Growth

The larval cultures were sampled every 48 h (10°C , 24 h (15, 20, 25 and 30°C) or 12 h (35, 40 and 45°C) from hatching to the beginning of the wandering stage. Between 15 and 20 larvae were washed, dried on tissue paper, wrapped in aluminium foil and dried in a vacuum oven at 60°C for 24 h before being weighed individually on a Sartorius electronic microbalance (Model 4125).

Respiration

Oxygen consumption and carbon dioxide evolution from individual larvae over 5 mg wet weight were measured in a Gilson respirometer at 15, 20 and 25°C with 10 replicates for each determination. Following measurements the animals were frozen and weighed wet.

Respiration of eggs and larvae less than 5 mg wet weight was measured using a gas chromatograph (Pye-Unicam GCD), following the procedure of Tadmor *et al.* (1971). The respiration vessels were held at 20°C and gas samples were taken after 3 h. Between 5 and 10 eggs or larvae were used in each determination of which there were five replicates.

Calorimetry

Samples for calorimetry were collected as for growth, and in addition, regular sampling continued through to the pupal stage. At emergence the adults and their puparial cases were collected. All samples were dried in a vacuum oven at 60°C for 24 h.

Attempts to produce pellets from dried larval material were unsuccessful since the samples expressed significant amounts of oil, and it was impossible to pelletize the puparia. Thus, both larvae and puparia were combusted uncompressed. The interior of the bomb was checked after each burn for any scattering of unburnt material from the sample, and the sample was rejected if this occurred.

Samples larger than 100 mg were combusted in a commercially available version of the Miller and

yne (1959) calorimeter. Smaller samples were run in a modified version of the Phillipson (1964) calorimeter. Between two and five replicate samples were burnt, depending on the availability of material.

The ash content of the material was determined independently by burning a sample in a muffle furnace at 500°C for 24 h. The results are expressed as kJ per ash free gram (afg).

Results

Growth curves

A logistic growth curve was fitted to the larval growth up to the beginning of the wandering stage. The function used was

$$W_t = \frac{a/b}{1 + e^{(c-a-t)}} \quad (1)$$

where W_t is dry weight (mg) at time t (h); a , b and c are constants and e the base of natural logarithms.

The constants have the following properties.

(1) $a/b = W_m$, the maximum weight attained, and growth increments are converted to a proportion of W_m (as they were in this study), then

$$a = b.$$

(2) c is a constant derived from the integration of the differential equation.

$$\frac{dW}{dt} = aW - bW^2. \quad (2)$$

Values for the constants can be derived from:

$$a = \ln \frac{W_2(W_m - W_1)/W_1(W_m - W_2)}{t_2 - t_1} \quad (3)$$

where t_x = time x , W_x = weight at time x , and $t_2 > t_1$ and $W_2 > W_1$, and,

$$c = \ln \frac{W_m - W_0}{W_0} \quad (4)$$

where W_0 = average weight of the eggs.

The constants a , b and c are time independent with a and $b > 0$. Table 1 shows the values of the constants and the significances of the fits of the curves to the data.

Effect of temperature on developmental rates

In Fig. 1, the reciprocal of the development time for the trophic stage (i.e. from hatching to the time at which more than 50% of the larvae had entered the wandering stage) in days has been plotted against temperature. These data can also be interpreted as the proportion of the development completed per day, and this has also been included. From the curve of the rate of development against temperature three quantities can be estimated. (1) the optimal temperature; (2) the developmental threshold temperature; and (3) the lethal temperature. Optimum temperature is defined here as that which allows maximum development rate, and is taken to be the highest value on the rate of development curves in Fig. 1.

Approximate values of the development threshold temperatures were obtained by fitting a linear regression to the ascending arm of the development curves, and taking the threshold temperature to be the intersection with the temperature axis. This was a choice of the simplest and most commonly used model in an analysis for which there are several models (Wigglesworth 1965). Lethal temperatures were simply taken as the next 5°C step over which growth would not occur. Table 2 shows these parameters for each species.

TABLE 1. Values for the constants of the logistic growth curve, when $W_m = 1$

Temp (°C)	<i>Lucilia cuprina</i>			<i>Calliphora stygia</i>			<i>Calliphora hilli</i>			<i>Calliphora vicina</i>		
	<i>a, b</i>	<i>c</i>	<i>P</i>	<i>a, b</i>	<i>c</i>	<i>P</i>	<i>a, b</i>	<i>c</i>	<i>P</i>	<i>a, b</i>	<i>c</i>	<i>P</i>
10				0.0194	6.3344	*	0.0224	4.7832	**	0.0163	6.0548	**
15	0.0340	6.9444	**	0.0546	6.5012	*	0.0736	5.0132	**	0.0476	6.2126	**
20	0.0548	6.9436	**	0.0550	6.2126	**	0.0767	4.9264	*	0.0635	6.3754	*
25	0.1162	6.5008	*	0.1052	6.2031	*	0.1164	4.9693	**	0.0891	6.1457	*
30	0.1550	6.9945	**	0.0767	6.1534	*	0.1316	4.7128	**	0.1122	6.1700	**
35	0.1490	6.9869	*	0.0689	5.2056	*	0.1322	4.7474	**			
40	0.2555	7.0135	**									

* $P < 0.05$ ** $P < 0.01$

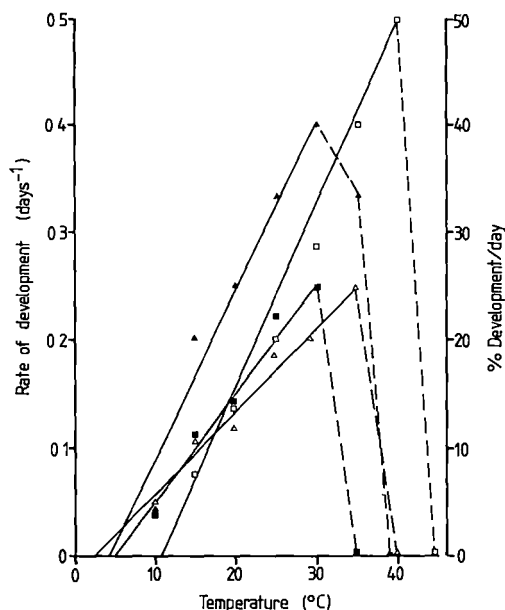


FIG 1 The rate of development as a function of temperature *C. hilli* ▲ *C. stygia* △ *C. vicina* ■ *L. cuprina* □ Solid lines represent linear regressions

Respiration

The results (expressed as $\mu\text{l O}_2$ consumed per individual per hour) were transformed to logarithms (base 10) and regressions calculated between the O_2 consumption and the wet weight of the animals. An analysis of the relationship between individual respiration rates and wet weight for feeding larvae is shown in Table 3 which gives the regression constants and the significances of the regressions. The following mean Q_{10} values were calculated over the range of temperature 15–25°C: *L. cuprina*, 1.381; *C. stygia*, 1.767; *C. hilli*, 1.571 and *C. vicina*, 1.232.

Respiratory quotients (RQ) calculated from the respiration rates at 20°C are shown in Table 4, for the various weight classes of feeding larvae, and for

TABLE 2. Optimal, lethal and developmental threshold temperatures (°C) for each species of blowfly

Species	Optimal	Developmental threshold	Lethal
<i>L. cuprina</i>	40	10	40–45
<i>C. stygia</i>	35	0.5	35–40
<i>C. hilli</i>	30	5	35–40
<i>C. vicina</i>	30	6	30–35

TABLE 3 Regression constants for the relationship between wet weight (x) and $\mu\text{l O}_2$ consumption per individual per hr (y) in the form $\log y = a + b \log x$

Species of larvae	a	b	P
<i>L. cuprina</i>	0.668	0.781	< 0.001
<i>C. stygia</i>	0.413	0.931	< 0.001
<i>C. hilli</i>	0.580	0.815	< 0.001
<i>C. vicina</i>	0.543	0.815	< 0.001

wandering larvae. The effect of synthesis while feeding is quite marked, with RQ values generally greater than one, indicating complex synthesis (Kleiber 1961). Wandering larvae, on the other hand, appear only to be catabolizing material, and the RQ values suggest that this is mainly protein (Petrusewicz & Macfadyen 1970).

Calorimetry

Table 5 gives the caloric densities of the feeding larvae and the pooled data gave the following caloric densities for each species: *L. cuprina* 23.87; *C. stygia* 24.98; *C. hilli* 27.32 and *C. vicina* 24.20 kJ afg^{-1} .

Caloric densities for the other life history stages and the shed puparia were compared within species. There were no significant differences except between the shed puparia of *L. cuprina* and the feeding larvae.

The energy budget

Weight specific instantaneous energy budgets were constructed for the feeding phase of the larvae of the four species, over their thermal tolerance ranges. All components were measured in $\text{kJ afg}^{-1}\text{h}^{-1}$. Growth rates, and thus production, were calculated with the

TABLE 4. RQ values for the weight classes of feeding larvae

Live weight class (mg)	<i>Lucilia cuprina</i>	<i>Calliphora stygia</i>	<i>Calliphora hilli</i>	<i>Calliphora vicina</i>
0–10	1.78	1.54	3.99	0.23
10–20	2.97	1.34	1.29	0.99
20–40	1.47	2.43	1.59	1.50
40–60	0.78*	1.89	—	1.01
60–80	—	1.07	2.37	—
80	—	0.84*	0.83*	0.88*

* wandering larvae (20 replicates for each case)

TABLE 5 Mean caloric densities (with standard deviations) for all the life history stages, and the size classes of feeding larvae. Caloric densities of the non-feeding stages are compared to the mean value for the feeding larvae

Stage	<i>Lucilia cuprina</i> (kJ afg ⁻¹)	<i>Calliphora stygia</i> (kJ afg ⁻¹)	<i>Calliphora hilli</i> (kJ afg ⁻¹)	<i>Calliphora vicina</i> (kJ afg ⁻¹)
Eggs (ovarine larvae of <i>C. hilli</i>)	25 0845±0 1930	17.6730±0 5938	17 1890±2 4609	19 1276±4 0015
Feeding larvae				
Size classes (mg d w)				
0-1	21 4125±1 5234	22 1118±0 2834	21 6944±0 8400	21 1035±1 3536
1-5	24 2919±0 9832	24 3243±0 8519	24 2375±0 5588	24 4587±1 7239
5-10	27 4905±2 6291	26 8170±2 0761	25 1040±1 3647	16 0769±2 4735
10-15	22 2921±0 5292	27 1953±0 9817	27 5403±1 8334	26 5232±0 7507
15-20		28 0399±0 1179	30 0458±0 0770	24 0024±2 8472
20-25		22 0279±2 7457	35 3060±5 1661	22 6910±3 6252
25		24 3315±0 6659		24 5696±1 8111
Mean value for feeding larvae	23 8718	24 9782	27 3213	24 2036
Wandering/quiescent larvae	27 1727	25 5018	30 1161	26 1873±0 5147
Pupae	28 0676	23 0532	25 7823±0 4510	28 3444
Puparia	10 2514±4 4693*	—	18 8699±0 4014	17 5913±3 9330
Emerged adults	27 0042±0 6469	—	27 5998±0 3066	23 6691±0 0838

* $P < 0.05$

logistic constants given in Table 1. As these relationships were based on dry weight of larvae and the regressions describing O_2 consumption were based on live weights, a set of allometric relationships for the conversion of live weight to dry weight were used (Williams unpubl. data).

An oxy-calorific coefficient was used to convert oxygen consumption to the amount of energy liberated. Since the RQ values previously calculated indicated that synthesis was occurring, no reliable indication of the materials being catabolised could be made. Consequently the general figure (0.79) suggested by Petruszewicz and Macfadyen (1970) for the catabolism of animal protein was used, which implies that the uptake of $218 \mu\text{l}$ of oxygen is equivalent to the release of $1.92 \times 10^{-5} \text{ kJ}$.

The Q_{10} values determined above were used to correct the respiration rates determined at 20°C to the rates expected at the range of temperatures used in calculation. The following parameters were calculated (Klekowski & Duncan 1975):

$$P_c = \int_{t_0}^{t_n} P(t) dt \approx \sum_{t_0}^{t_n} P \quad \text{cumulative production,}$$

$$R_c = \int_{t_0}^{t_n} R(t) dt \approx \sum_{t_0}^{t_n} R \quad \text{cumulative respiration,}$$

$$A_c = P_c + R_c \quad \text{cumulative assimilation,}$$

where t_0 = time at hatching,
and t_n = time at end of feeding stage;

$$P_i = \frac{dP}{dt} \quad \text{instantaneous rate of production,}$$

$$R_i = \frac{dR}{dt} \quad \text{instantaneous rate of respiration,}$$

$$A_i = P_i + R_i \quad \text{instantaneous rate of assimilation}$$

From these parameters the following non-dimensional indices were calculated;

$$K_{2c} = \frac{P_c}{A_c} 100 \quad \text{cumulative growth efficiency}$$

$$K_{2i} = \frac{P_i}{A_i} 100 \quad \text{instantaneous growth efficiency}$$

and

$$M_i = \frac{R_i}{P_i} \quad \text{instantaneous cost of maintenance,}$$

As A_i is derived from P_i and R_i , only A_i has been presented here in Figs 2 (a-d) plotted against body weight and temperature. It should be noted that at the end of the feeding stage, the energy budget goes into deficit as larvae stop feeding and $P_i = 0$, thus $A_i = R_i$. It can be seen from Figs 2 (a-d) that A_i increases with temperature, within the temperature tolerance range of the larvae. This is due in part to increasing respiratory costs (R_i), and since P_i also increases with temperature, consumption and digestion rates must increase. However, as consumption and rejection were not measured here, this suggestion cannot be verified.

The effect of temperature on the weight specific instantaneous conversion efficiencies, K_{2i} and M_i , can be seen in Figs 3 (a-d) and Figs 4 (a-d), respectively. From Figs 3 (a-d) it can be seen that 25°C represents an optimum for production in all species. The value of K_{2i} for *L. cuprina* is relatively independent of temperature above 25°C . Indeed there is an increase in K_{2i} at 40°C . However, below 25°C , there is a dramatic decline in K_{2i} . In contrast, all the *Calliphora* species show great sensitivity in

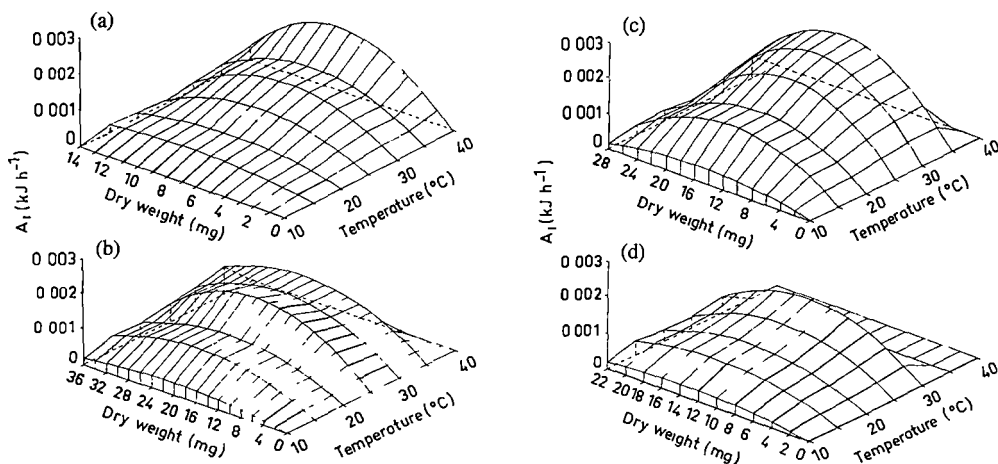


FIG. 2. The estimated values of the instantaneous assimilation rate (A_i) against temperature and body weight: (a) *L. cuprina*, (b) *C. stygia*, (c) *C. hulli*, (d) *C. vicina*.

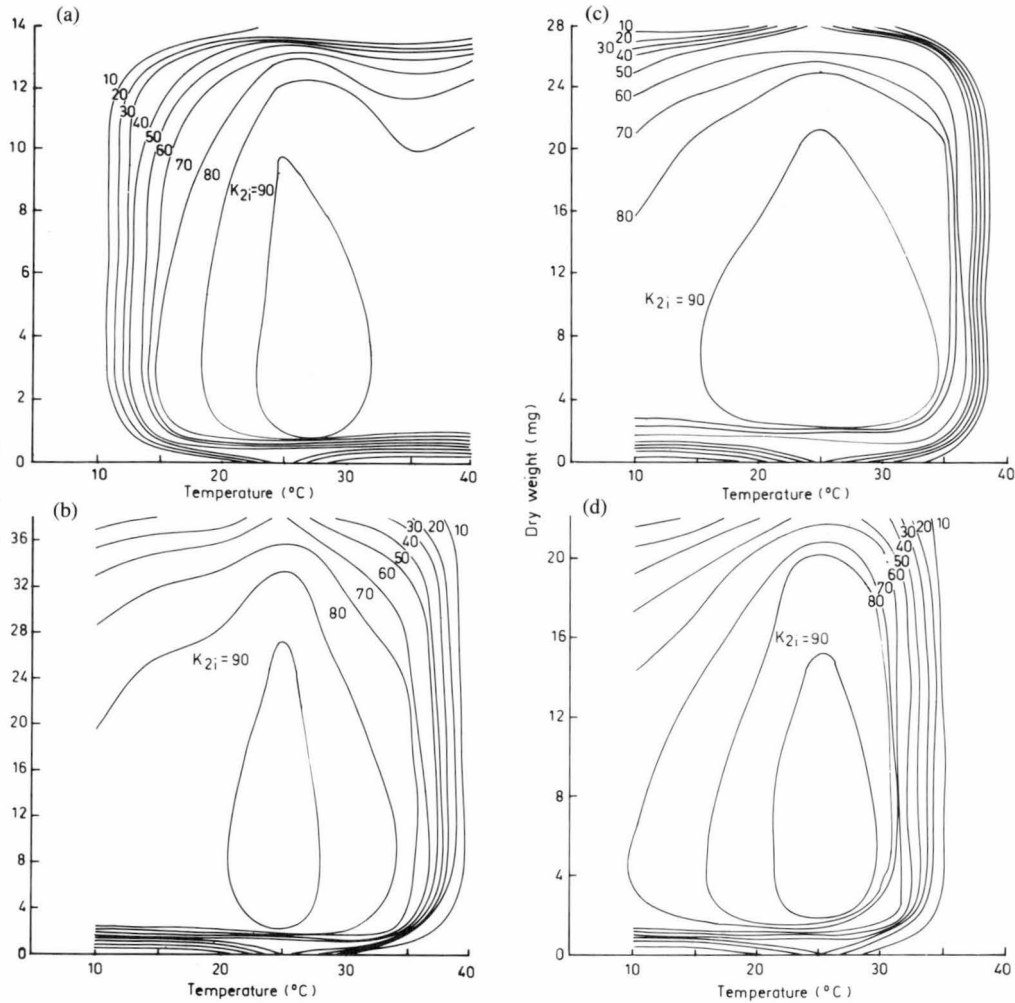


FIG. 3. Contour plots of the estimated values of the instantaneous growth efficiency (K_{2i}) against temperature and body weight. The contour lines are labelled with the corresponding value of K_{2i} for each level. (a) *L. cuprina*, (b) *C. stygia*, (c) *C. hilli*, (d) *C. vicina*.

the effect of temperatures above 25°C on K_{2i} with rapid decreases in efficiency with increased temperature. At temperatures below 25°C, the reverse of the effect seen for *L. cuprina* occurs, with K_{2i} exhibiting an independence from temperature except at the very end of the feeding stage.

Generally it appears that small larvae (2–6 mg *L. cuprina* and 4–12 mg *Calliphora* spp.) show greater independence of K_{2i} with temperatures around $25 \pm 5^\circ\text{C}$. The greatest independence is seen for *C. hilli*, which maintains optimal K_{2i} over the range 15–35°C.

On the cost side of the energy budget, the plot of M_i against body weight and temperature show much the same pattern as for K_{2i} . The relative inde-

pendence of M_i at temperatures above 25°C for *L. cuprina* and the increase at 40°C are again seen. The dependence of M_i on temperatures below 25°C reflecting increasing maintenance costs is repeated. The contrast of *L. cuprina* with the *Calliphora* species takes the same form, with all the *Calliphora* species showing a relative independence of M_i on temperatures below 25°C and dependence above 25°C.

Whereas K_{2i} was maintained at an optimal level over a wide range of temperatures for small larvae, M_i shows much greater sensitivity to temperature. Optimal conditions occur only at 25°C for small larvae and fall rapidly from this point. Larvae reaching the end of the feeding stage exhibit high main-

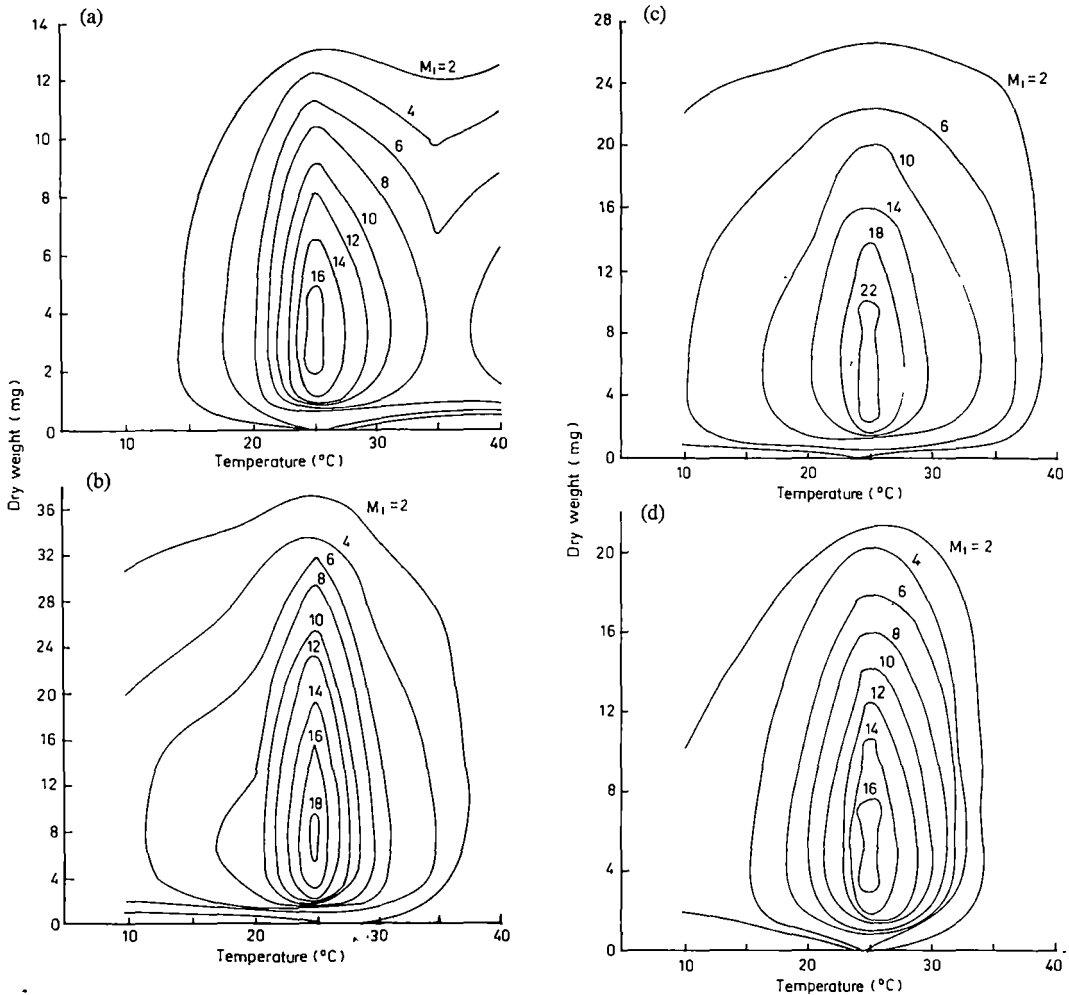


FIG. 4 The estimated values of the instantaneous cost of maintenance (M_1) against temperature and body weight. The contour lines are labelled with the corresponding value of M_1 for each level. (a) *L. cuprina*, (b) *C. stygia*, (c) *C. hilli*, (d) *C. vicina*.

tenance costs as their respiratory costs increase while production falls.

The cumulative growth efficiency (K_{2c}) was calculated from the cumulative energy budget (Appendix 1). When the effect of temperature on the value of K_{2c} for the larvae, over their thermal tolerance ranges (Fig. 5), is compared to M_1 and K_{2i} , we see again that 25°C represents an optimum, and that whilst K_{2c} falls at temperatures on either side of this optimal temperature, there are secondary inflections showing increases in K_{2c} at 40°C for *L. cuprina*, and at 10°C for *C. stygia* and *C. vicina*. No secondary peak is apparent for *C. hilli* but the decline in K_{2c}

between 15 and 25°C is substantially less than that of the other *Calliphora* species resulting in a similar value of K_{2c} at 10°C.

The general trends show that energy conversion to the production of tissue in all the species is optimal at 25°C. In the *Calliphora* species, optimal energy conversion is 'cold' adapted with high production and low maintenance costs maintained relatively independent of lower temperatures. In contrast, *L. cuprina* is 'warm' adapted, performing poorly at low temperatures, but exhibiting high production efficiencies and low maintenance at high temperatures.

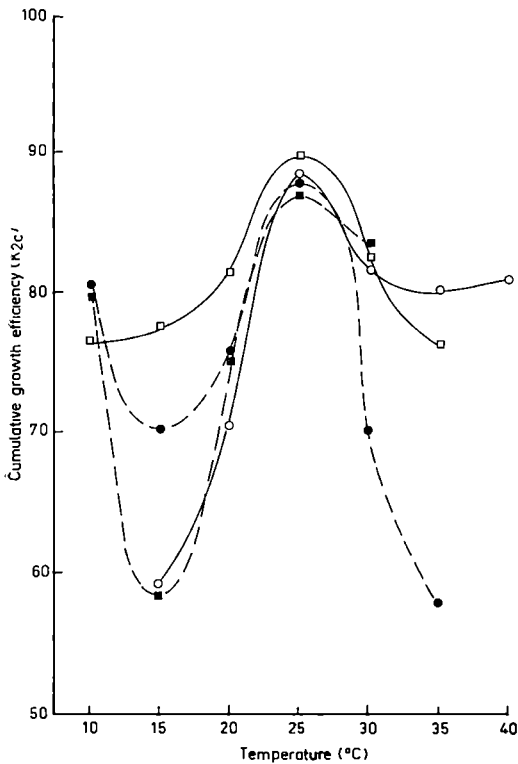


FIG. 5 The estimated values of the cumulative growth efficiency (K_{2c}) over the thermal tolerance ranges of the four species of feeding larval *L. cuprina* ○, *C. stygia* ●, *C. hilli* □, *C. vicina* ■

Discussion and conclusions

Energetics of blowfly larvae

Hanski (1977) determined a cumulative growth efficiency (K_{2c}) of 77% for *Lucilia illustris* (Meigen), grown under fluctuating temperatures. This figure lies in the range of K_{2c} values determined in this study under constant temperature conditions. He suggested that under fluctuating temperatures, K_{2c} was reduced by about 10%, and if this is included in his value, the amount (c. 85%) agrees with the efficiencies presented here for temperatures from 20 to 30°C.

Hanski (1976) surmised that the highest values of the instantaneous growth efficiency (K_{2i}) correspond to the most intense phase of growth. The results presented here support this hypothesis as the highest K_{2i} values occur over the range of weights where P_1 is increasing. K_{2i} then declines as P_1 declines. Hanski (1976) also suggested that there was

an optimum temperature for the allocation of assimilated energy to production should exist, and that K_{2i} in the most intensive growth phase should be relatively temperature independent. Both these suggestions are supported here: 25°C represents an optimum in K_{2i} for all species, and there is evidence that smaller larvae (undergoing the most intensive growth rates) exhibit greater independence in K_{2i} with regard to temperature about this optima.

In his study of the energetics of blowfly larvae in carrion, Putman (1977) used a respiratory quotient value (RQ) derived from the average for feeding, prepupal and pupal stages. We did not consider this value (0.878) to be applicable to feeding larvae due to the different catabolites used in the feeding and non-feeding pupal stages, i.e. proteins and fats, respectively (Thomson 1975). In order to minimize errors, a generalized RQ for the metabolism of animal protein (0.79) was used here for calculations involving feeding larvae, thus removing the bias inherent in Putman's calculations.

Assimilation rates of larvae of *C. vicina* are given by Putman (1977). Although the figures presented here are consistently lower than his, they lie within his standard deviations. The disparity may be due to the fact that Putman did not calculate production directly from production curves, and did not account for the cost of maintenance in the atrophic pupal stages.

Reproductive strategies

Egg size and the average energy content of the eggs (Table 6), can be ranked from lowest to highest:

L. cuprina < *C. vicina* < *C. stygia* < *C. hilli*.

Adult females can allocate their energy reserves into two major areas, reproduction which involves the production of egg material, and maintenance which includes locomotion. Because only a finite amount of energy can be allocated to reproduction a species has the choice of producing a few large propagules or many small propagules (Smith & Fretwell 1974; Calow 1978). The size of the propagules can theoretically be related to their 'fitness', since large propagules should have a greater probability of survival than small propagules. If the number of propagules produced in one batch (i.e. in one cycle of ovarian development) by females of a similar size (Table 6) is ranked from highest to lowest then the order seen above is reversed:

L. cuprina > *C. vicina* > *C. stygia* > *C. hilli*

egg size can be seen to be inversely proportional to batch size, as theory suggests.

TABLE 6 Egg sizes, fecundity and energy allocation to propagules in the four blowfly species Number of eggs from Williams and Richardson (1983)

	<i>L. cuprina</i>	<i>C. stygia</i>	<i>C. hilli</i>	<i>C. vicina</i>
Egg dry weight (mg)	0.026	0.058	0.180	0.048
Number of eggs produced by ♀♀ of 16 mg dry weight (a)	343	85	72	111
kJ propagule ⁻¹ ($\times 10^{-5}$) (b)	65.22	102.5	309.4	91.81
Energy content of clutch kJ (a \times b)	0.224	0.087	0.223	0.102

A similar ranking can be seen when the caloric density of the eggs (Table 5) is substituted for size.

L. cuprina > *C. vicina* > *C. stygia* > *C. hilli* this relationship is interesting as it suggests that reduction in egg size, (and hence the 'fitness' of the propagule) is compensated by improved egg quality.

The relationship between batch weight and the adult's reproductive strategies has been discussed elsewhere (Williams & Richardson 1983) for these species.

The effects of temperature on species success in carrion

The interaction between temperature and metabolic rates which are differentially affected by temperature is well established in the literature (e.g. Keister & Buck 1964; Wigglesworth 1965). As well as the interaction between differential increases in growth efficiencies, cost of maintenance and temperature, a third set of temperature-dependent processes is important: feeding and digestive rates (Brown 1957; Weatherly 1976).

While the results presented here demonstrate a relative fall in the cumulative growth efficiency (K_{2c}) and the instantaneous cost of maintenance (M_1) for all larvae at temperatures greater than 25°C, their increased rates of development are almost certainly attributable to an increase in their rates of consumption. Interpretation of optimal temperatures is therefore complicated as although the rates of development of all larvae are highest at temperatures greater than 25°C, the K_{2c} values in all cases is highest at 25°C.

Hanski (1977) has demonstrated that the temperature history of larvae can affect their development time by acting on net growth efficiency at critical phases in the growth period, e.g. the initial growth phase or the period of rapid growth at the beginning of the third instar. He found that fluctuating temperatures lowered K_{2c} and from this he suggested that the differences in arrival times of eggs at carrion

(and thus the different times during development at which temperatures will act) would be great enough to create a mosaic of competition events due to chance factors involved in the arrival of the species at carrion. Hanski also pointed out that a general increase in temperature would increase the importance of the initial species composition in determining the success of species emerging from carrion which he termed the 'priority effect', while a decrease in temperature would have the reverse effect. The temperature regimes considered by Hanski were in the range found in normal daily fluctuations and did not approach upper lethal limits.

On the basis of Hanski's hypothesis, one would expect that at low temperatures, *L. cuprina*'s lower assimilation efficiency and rate of development would put it at a disadvantage whether it is an early arrival at the carcass or not. But at higher temperatures this effect would be reduced, since as a primary fly, *L. cuprina* can be assumed to be an early starter. At temperatures greater than 35°C, which is above the highest temperature which Hanski considered (33°C), *L. cuprina* is the only species which can grow and produce viable wandering larvae.

A reappraisal of the role of Lucilia cuprina in carrion

The results presented here suggest that *L. cuprina* should be a successful competitor amongst the flies compared in carrion when carcass temperatures are elevated in excess of 30°C. However, from field observations made in south-eastern Australia, Mackerras (1936) proposed that the *Calliphora* species outcompete *L. cuprina* in carrion, and Waterhouse (1947) considered that the temperatures generated by *Ch. rufifacies* would be intolerable for *L. cuprina*.

To clarify this apparent disagreement with the findings of Mackerras (1936) and Waterhouse (1947), we can consider two observations. The first, from Waterhouse's record of the temperatures

occurring within a dead sheep, is that in large carcasses temperatures up to 42°C (or even 49°C : Vogt & Woodburn 1979) develop, and at these temperatures *L. cuprina* is not considered to be "successful" (Waterhouse 1947). The second is the observation that sheep which die of complications due to myiasis produce significantly more *L. cuprina* than sheep colonized *post mortem* (Norris 1959).

The first case will not occur in areas where *Chrysomya* species are absent (e.g. southern Tasmania) as all the species which occur in carrion except *L. cuprina* will be disadvantaged at high temperatures. *L. cuprina*'s poor performance on the mainland can be attributed to the presence of *Chrysomya rufifacies*, which is known to tolerate the higher temperatures (and is implicated in elevating them), and is predatory on small larvae (Waterhouse 1947).

The second case occurring on the Australian mainland, in areas where *Chrysomya* species are present, may be explained by Hanski's "priority effect", in that a strike will most probably be purely by *L. cuprina* (Watts *et al.* 1976) and with cooling after death the carcass would be ideally suited to the larvae already established. Cooling should not occur to a degree that would significantly disadvantage *L. cuprina* since the minimum temperature which Waterhouse (1947) recorded in a carcass was 15°C, even though the recordings were made in winter when ambient temperatures are lower than during the activity period of *L. cuprina*. Furthermore, this minimum temperature was recorded before any larvae had appeared to raise the temperature of the carcass. By the time that larvae of *Ch. rufifacies* are present, they would have little effect on the development of *L. cuprina*. The *L. cuprina* larvae would be close to the end of their growth period, and thus unlikely to be subjected to the high temperatures generated by the activity of *Ch. rufifacies* for any significant length of time, and unsuitable for predation, being too large.

In conclusion, the two identified causal mechanisms for *L. cuprina*'s poor performance in carrion (i.e. the presence of *Ch. rufifacies* and superior competition at elevated temperatures by other calliphorids) do not apply in southern Tasmania, and probably only to a small degree in Tasmania as a whole. Indeed, on the criteria described in this study, *L. cuprina* appears to be the best suited species for the exploitation of large carcasses.

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References

- Brown M. E. (1957) *The Physiology of Fishes Volume I, Metabolism*. Academic Press, London.
- Calow P. (1978) *Life Cycles: An Evolutionary Approach to the Physiology of Reproduction, Development and Aging*. Chapman & Hall, London.
- Denno R. F. & Cothran W. R. (1976) Competitive interactions and ecological strategies of Sarcophagid and Calliphorid flies inhabiting carrion. *Ann. ent. Soc. Am.* **69**, 109–13.
- Hanski I. (1976) Assimilation by *Lucilia illustris* (Diptera) larvae in constant and changing temperatures. *Oikos* **27**, 288–99.
- Hanski I. (1977) An interpolation model of assimilation by larvae of the blowfly, *Lucilia illustris* (Calliphoridae) in changing temperatures. *Oikos* **28**, 187–95.
- Keister M. & Buck J. (1964) Respiration: some exogenous and endogenous effects on rate of respiration. In *The Physiology of Insecta* (ed. M. Rockstein) pp. 617–58. Academic Press, New York.
- Klekowski R. Z. & Duncan A. (1975) Physiological approach to ecological energetics. In *Methods for Ecological Bioenergetics* (eds W. Grodzinski, R. Z. Klekowski and A. Duncan) pp. 15–64. IBP Handbook No. 24. Blackwell Scientific Publications, Oxford.
- Kleiber M. (1961) *The Fire of Life: An Introduction to Animal Energetics*. J. Wiley, New York.
- Mackerras I. M. (1936) The sheep blowfly problem in Australia. results of some recent investigations. CSIRO (Aust.) Pamphlet 66.
- Miller D. S. & Payne P. A. (1959) Ballistic bomb calorimeter. *Br. J. Nutr.* **13**, 501–8.
- Norris K. R. (1959) The ecology of the sheep blowfly in Australia. *Mongr. Biol.* **8**, 514–44.
- Payne J. A. (1965) A summer carrion study of the baby pig *Sus scrofa* Linnaeus. *Ecology* **46**, 592–602.
- Petrusewicz K. & Macfadyen A. (1970) *Productivity of Terrestrial Animals: Principles and Methods*. IBP Handbook No. 13. Blackwell Scientific Publications, Oxford.
- Phillipson J. (1964) A miniature bomb calorimeter for small biological samples. *Oikos* **15**, 130–9.
- Putman R. J. (1977) Dynamics of the blowfly *Calliphora erythrocephala* within carrion. *J. Anim. Ecol.* **46**, 853–66.
- Putman R. J. (1978) The role of carrion-frequenting arthropods in the decay process. *Ecol. entomol.* **3**, 133–9.
- Roback S. S. (1951) A classification of the muscoid calypterate Diptera. *Ann. ent. Soc. Am.* **44**, 327–61.
- Ryan A. F. (1954) The sheep blowfly problem in Tasmania. *Aust. Vet. J.* **30**, 109–13.
- Smith C. C. & Fretwell S. D. (1974) The optimal balance between size and number of offspring. *Am. Nat.* **108**, 499–506.
- Tadmor U., Applebaum S. W. & Kafir R. (1971) A gas-chromatographic micromethod for respiration studies on insects. *J. Exp. Biol.* **54**, 437–41.

Ulyett G C (1950) Competition for food and allied phenomena in sheep blowfly populations *Phil Trans Roy Soc Lond Ser B* **234**, 77–175

Vogt W G & Woodburn T L (1979) Ecology, distribution and importance of sheep myiasis flies in Australia *National Symposium on the Sheep Blowfly and Flystrike in Sheep* NSW Department of Agriculture, Sydney

Waterhouse D F (1947) The relative importance of live sheep and of carrion as breeding grounds for the Australian sheep blowfly *Lucilia cuprina* CSIRO (Aus) Bull. **217**.

Watts J E , Muller M J , Dyce A L & Norris K R (1976) The species of flies reared from struck sheep in south eastern Australia *Aust Vet J* **52**, 488–9

Weatherley A H (1976) Factors affecting maximization of fish growth *J Fish Res Board Can* **33**, 1046–58

Wigglesworth V B (1965) *The Principles of Insect Physiology* Methuen, London

Williams H & Richardson A M M (1983) Life history responses to larval food shortages in four species of necrophagous flies (Diptera Calliphoridae) *Aust J Ecol* **8**, 257–63

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Appendix 1. Cumulated parameters for production (P_c), respiration (R_c) and assimilation (A_c) of feeding larvae over the experimental temperature range.

Species	Cumulative parameter	Temperature (°C)						
		10	15	20	25	30	35	40
<i>L. cuprina</i>	P_c	—	0 3268	0 3280	0 3282	0 3284	0 3289	0 3291
	R_c	—	0 2932	0 1291	0 0423	0 0642	0 1014	0 0801
	A_c	—	0 6199	0 4571	0 3705	0 3926	0 4303	0 4092
<i>C. stygia</i>	P_c	0 9336	0 9331	0 9329	0 9326	0 9330	0 9332	—
	R_c	0 0801	0 3759	0 3277	0 1511	0 4165	0 6916	—
	A_c	1 0137	1 3090	0 9606	1 0837	1 3495	1 6248	—
<i>C. hilli</i>	P_c	0 6531	0 7343	0 7344	0 7337	0 7351	0 7351	—
	R_c	0 1807	0 2022	0 1527	0 6784	0 0420	0 2124	—
	A_c	0 8338	0 9365	0 8871	1 4121	0 7771	0 9475	—
<i>C. vicina</i>	P_c	0 1293	0 5317	0 5317	0 5323	0 5321	—	—
	R_c	0 0338	0 3774	0 1748	0 0777	0 1232	—	—
	A_c	0 1631	0 9091	0 7065	0 6100	0 6553	—	—

Modification of the West Australian Blowfly (Diptera: Calliphoridae) Trap for Population Studies

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ABSTRACT In view of the expense of construction of the standard "West Australian" (WA) bait trap, a new model is described for use in population studies of necrophagous calliphorid flies, particularly *Lucilia cuprina* (Wiedemann). The new version uses the same principle as the WA bait trap but takes advantage of modular plastic products in its fabrication. Data are presented for calibration of the new trap compared with the standardized WA bait trap.

The "West Australian" (WA) bait trap was originally described by Newman and Clark (1926) and standardized for population studies by Gilmour et al. (1946). Improvements to the standard design were made by Vogt and Havenstein (1974). The trap is now widely used in blowfly population studies, even though the sample is heavily biased to the phases of adult flies which are actively searching for protein.

As shown by Vogt and Havenstein (1974), the standard WA bait trap is expensive in both materials and construction. At current prices, one trap costs ca. 130 Australian dollars (A\$130) in materials and labor. Assuming that 10 to 12 replicate traps are needed for a population survey, a minimum outlay of A\$1,300 is required.

The trap described here uses polyvinylchloride (PVC) components produced for the plumbing trade. These components are cheap, give greater rigidity to the overall structure, and are easy to replace. The design employs the same principle as the standard WA bait trap; however, components cost ca. A\$5.00, and each trap requires about 1 h to fabricate.

Materials and Methods

The assembled trap is illustrated in Fig. 1, and a vertical section is shown in Fig. 2.

The fly chamber is constructed from an opaque plastic, 4.5-liter, screw-top jar (Australian Consolidated Industries International P/L.Y23-143). Four windows (15 by 11 cm) are cut into the sides of the jar, and glass fiber fly screening (mesh size = 18 cm) is applied over these by "welding" the screen to the plastic with a soldering iron. A small hole (3 mm in diameter) drilled into the center of the base of the jar provides an opening permitting a wire hook to pass for attaching the trap to the ground.

The cone is also constructed from glass fiber screening; a sheet metal template serves as a cutting guide. The cones are stapled together and held

in place between the lip of the jar and the jar's lid, in which a hole 8 cm in diameter has been made. The jar's lid is cemented with PVC glue to the inside of the entry chamber. Because the lid's

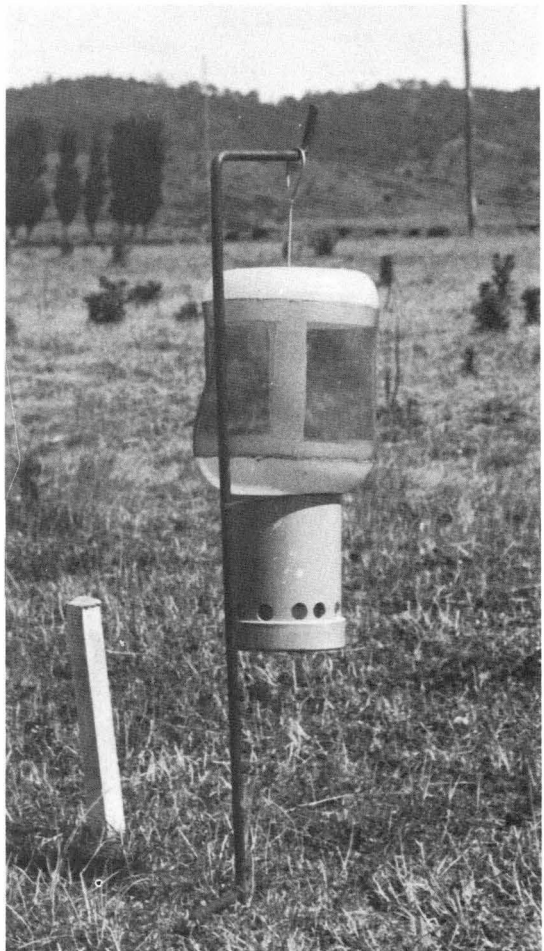


Fig. 1. Assembled trap in place in the field.

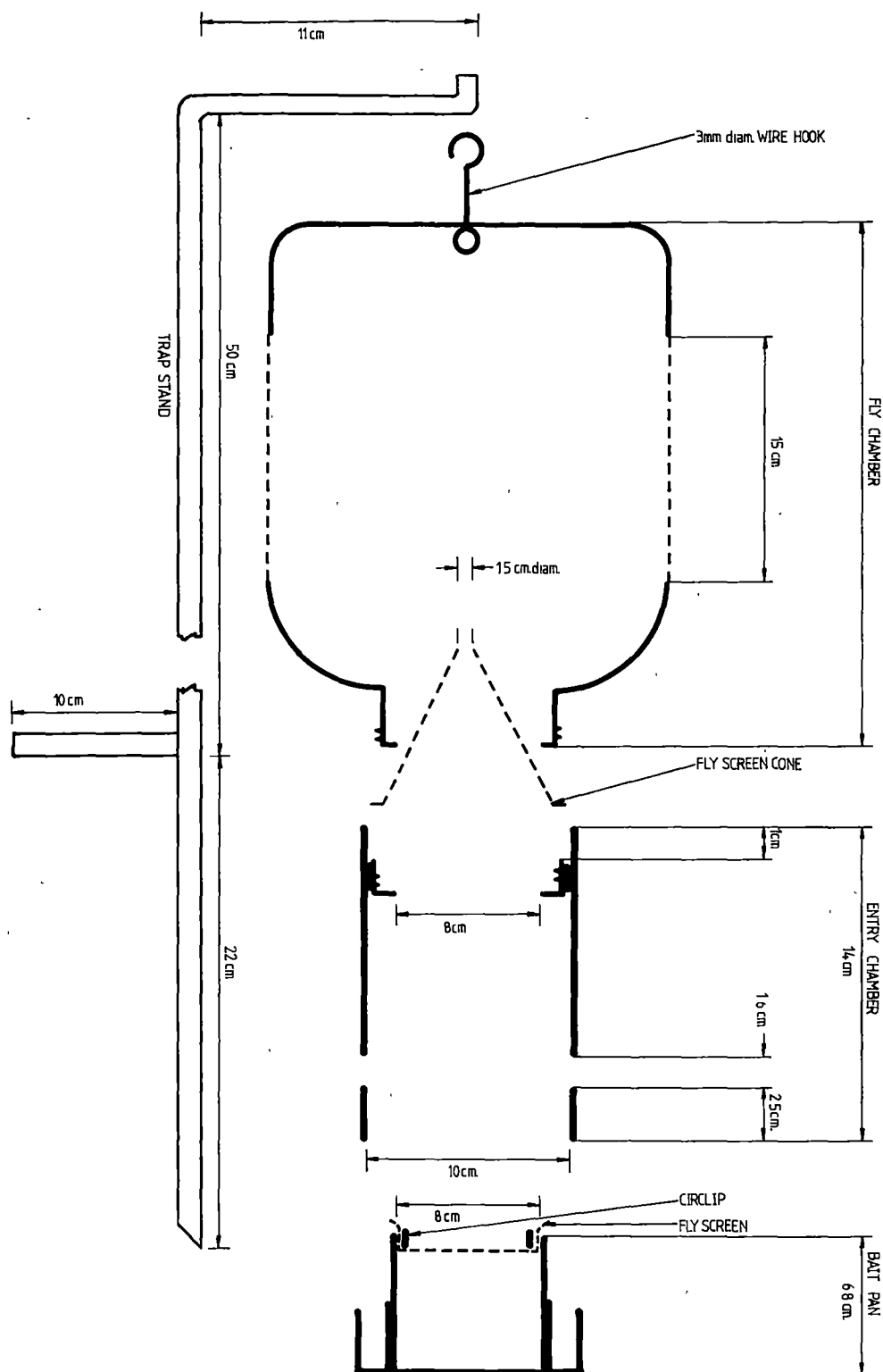


Fig. 2. Exploded, vertical section of the trap and trap stand. Broken lines represent glass fiber fly screening

Table 1. Comparison of the two models of blowfly traps for sampling four major blowfly species on a sheep at Powranna, Tasmania

Trap model	Mean no. of species caught/trap ^a				No. of traps	Bait/	
	<i>L. cuprina</i>	<i>L. sericata</i>	<i>C. stygia</i>	<i>C. hilli</i>		Liver (g)	sodium sulfide solution (ml)
WA bait trap	135.4	174.0	9.3	9.8	7	1,500	1,000
Modified design of Williams	42.1	17.1	16.4	2.4	10	50-60	30

^a Values represent mean catch per trap collected on 3 April 1983 from 0900 to 1700

outside diameter is less than the internal diameter of the entry chamber, a filler ring made from off-cuts of the piping used for the entry chamber is used.

The entry chamber consists of a 14-cm length of storm water and vent (SWV) 10-cm PVC pipe. The jar's lid is glued into this to a depth at which the bottom lip of the lid is 1 cm below the cut edge of the pipe. Ten holes, 1.6 cm in diameter each, are drilled around the other end of the pipe, with the bottom edge of the holes 2.5 cm from the end (this is done so that the holes are not obscured when the push-on cap is in place).

The 10-cm PVC push-on caps (Hardie Iplex S38), have an 8-cm center well, which serves as a bait receptacle. A length of SWV 8-cm PVC pipe (6.4 cm long) is cemented into this well.

To exclude flies from the bait, a circle of fly screening (10 cm in diameter) is fixed inside the top of the bait pan with a cir-clip made from a thin off-cut of the 8-cm pipe with a 3-cm length cut from its wall. Fixing fly wire over the top of the bait pan with a rubber band or similar device is not recommended, because this reduces the clearance between the entry holes and the sides of the bait pan (which is ca. 1.6 cm), and thus may hamper the flies' access to the main body of the entry chamber.

The trap is hung by the hook at the top of the fly chamber from a stand made of 10-mm black round steel. The stand is 72 cm in length; a cross-piece welded on at 22 cm from the angle cut end acts as both a convenient means of inserting the end into hard ground and a spacer ensuring that the arm at the top will be 50 cm above the ground. The arm is 18 cm in length including the upturned end, so the arm is easily bent starting with a piece of steel 90 cm long. A rubber band can be put around the stand and entry chamber to prevent the trap from swinging in the wind.

The bait pan and entry chamber are painted yellow to increase the attractiveness of the trap to blowflies, in a manner similar to the standard WA bait trap. The new model is baited with the same bait as specified for the standard WA bait trap (Vogt and Havenstein 1974). However, the volume of the bait is reduced, from 1.5 kg of liver in

a 1-liter sodium sulfide solution (standard WA bait trap) to 50 to 60 g of liver in a 30-ml sodium sulfide solution (new model). The sodium sulfide solution enhances and prolongs the attractiveness of the bait to primary blowflies; it is prepared by adding 20 g of crystalline sodium sulfide to 1 liter of water (Vogt and Havenstein 1974).

Results and Discussion

The traps were used in a summer trapping program during the 1982-1983 season. In the course of ca. 2,200 trap-hours of operation, minor repairs were required only twice. The new trap model required 5 min to open and 10 min to close (including time for killing and bottling flies).

No ants interfered with the operation of the new model. However, if ants pose a problem, application of grease at the base of the stand should satisfactorily block access to the trap.

A field trial was conducted on 3 April 1983 to compare the new trap with the standardized WA bait trap. Two adjacent trapping grids were established on a sheep farm at Powranna in central Tasmania, with seven standard WA bait traps on one grid and 10 of the new model on the other. The two types of traps were opened and closed simultaneously at 0900 and 1700, respectively. All *Lucilia* spp. and *Calliphora* spp. were counted, and the mean catch per trap is given in Table 1.

The new trap caught ca. 0.33-fold the *L. cuprina*, 0.1-fold the *Lucilia sericata* (Meigen), 1.7-fold the *Calliphora stygia* (F.), and 0.25-fold the *Calliphora hilli* Patton caught by the WA bait trap. Considering the reduction in bait mass (0.03-fold that of the WA bait trap), the new trap is more bait per catch effective.

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References Cited

- Colman, D., D. F. Waterhouse, and G. A. McIntyre. 1974. An account of experiments undertaken to estimate the natural population of the sheep blowfly *Lucilia cuprina* (Wied.) Bull. Coun. Sci. Ind. 13: 249-253.
- Vogt, W. G., and D. E. Havenstein. 1974. A standardised bait trap for blowfly studies. J. Aust. Entomol. Soc. 13: 249-253.
- Newman, L. A., and J. Clark. 1926. Trapping blowflies. J. Dep. Agric. W. Aust. 3: 382-391.

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